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THE GENERA OF THE EBENALES IN THE SOUTHEASTERN UNITED STATES ¹

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OF THOSE COMPRISING THE EBENALES in the Englerian sequence of angiosperm families, four — Sapotaceae, Ebenaceae, Styracaceae, and Symplocaceae — occur in the southeastern United States, and it is these which are considered here as constituting the order. These four families, together with the Hoplestigmataceae, Diclidanthaceae, and Lissocarpaceae, also included by Engler and Gilg, are characterized by sympetalous corollas with stamens generally two or three times as many as the corolla lobes (or, by abortion, equal in number to and opposite them) and by superior to inferior, incompletely to completely loculed ovaries with axile placentation.

Wettstein, Engler and Gilg, Rendle, Cronquist, and Benson, among others, have retained the four larger families in a single order (although sometimes with additions), but others, as Hallier and Hutchinson, have split the group in various ways. Copeland (see Styracaceae) suggests that the order is a natural group with a collateral relationship to the Ericales and with an ancestry most nearly represented among living plants by the Theaceae. Altogether, the evidence from floral morphology and anatomy, pollen, wood structure, nodal anatomy, and embryology, insofar as this information is available, is in harmony with this view, and no very convincing data have yet been presented to the contrary. Various items in the

¹ Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation. The scheme follows that outlined at the beginning of the series (*Jour. Arnold Arb.* 39: 296–346. 1958). Other published portions of these studies will be found in *Jour. Arnold Arb.* 40: 94–112, 161–171, 268–288, 369–384, 391–397, 413–419. 1959, and in the present issue. We are much indebted to the many people who have given freely of advice, information, or materials in connection with the four families treated here. In addition to our immediate colleagues, these include L. J. Brass, G. R. Cooley, W. H. Duncan, R. J. Eaton, R. K. Godfrey, Mrs. J. N. Henry, J. Kucyniak, J. D. Ray, Jr., H. W. Rickett, H. F. L. Rock, H. St. John, W. T. Stearn, F. A. Stafleu, and Mrs. C. E. Wood. The data on nodal anatomy are from the unpublished petiolar studies of R. A. Howard and are used with his kind permission. As in previous papers in this series, the illustrations are the work of Dorothy H. Marsh.

descriptions and discussions which follow will be found to bear on this problem.

At least some of the characteristics which often are cited in connection with the interrelationships of the families of the Ebenales need qualification and a great deal more investigation. For example, although the Sapotaceae are said to have completely septate ovaries, those of at least some (e.g., species of *Bumelia* and *Manilkara*) are at anthesis septate below but are no more completely so above than those of *Styrax*, and in inferior ovaries in both Styracaceae and Symplocaceae a similarly incomplete condition occurs. Moreover, that inferior ovaries characterize five of the thirteen genera of the Styracaceae usually is glossed over in comparisons with the Symplocaceae. It should be remarked, too, that in the Ebenaceae, a single ovule in each locule seems to occur much more frequently than two, and there are indications that this condition may have come about through the development of additional septa which have separated the paired ovules. Indeed, all four families may well provide examples of increase in numbers of flower parts, rather than reduction. (Cf. the perianth and gynoecium of Sapotaceae and Ebenaceae and the androecium of Styracaceae and Symplocaceae, for example.) It is also noteworthy in connection with phylogeny that the ovules of Sapotaceae seem to have a single integument, those of Ebenaceae two, of Styracaceae either two or one (by fusion of the two), and of Symplocaceae one, although as yet very few representatives of these families have been examined.

SAPOTACEAE (SAPOTE FAMILY)

Armed or unarmed trees or shrubs with milky sap and alternate [rarely opposite], simple, exstipulate, usually entire and coriaceous leaves, the nodes with 3 traces from 3 leaf-gaps (except some species of *Bumelia*, 1 from 1). Inflorescences axillary, basically dichasial, ours simple, cymose or umbellate, or the flowers sometimes singly disposed, the pedicels bracteolate at the base. Flowers complete, regular. Calyx of 4-9 [-12] imbricate, biseriate, or spirally arranged sepals, connate at the base. Corolla sympetalous, the lobes imbricate in the bud, usually as many as the sepals, sometimes with paired lateral or dorsal appendages. Stamens [twice as many as or] as many as and opposite the lobes of the corolla, epipetalous, distinct, the anthers 2-locular, longitudinally dehiscent; staminodia (when present) alternate with the fertile stamens and the lobes of the corolla. Gynoecium syncarpous, the style 1, the stigma unlobed or with as many lobes as locules, the ovary superior, the locules 1-14, typically 4 or 5, the placentation axile, a single, anatropous, 1-integumented ovule in each locule [except in *Diploön* with unilocular ovary and 2 ovules]. Fruit an indehiscent berry, often with a thin, leathery to bony outer layer; seeds large, with fleshy endosperm or none. TYPE GENUS: *Sapota* Mill. = *Manilkara* Adans.

A family of about 40 genera and more than 600 species, all woody, and primarily of the tropics of both hemispheres. Six of the approximately 15

genera of the Western Hemisphere are represented in the southeastern United States, but only *Bumelia* occurs outside of peninsular Florida in this area.

The Sapotaceae are distinguished from the other families of the Ebenales by the superior ovary which is usually completely septate (note illustration of *Bumelia*, however) and by the presence of a solitary ascending, 1-integumented ovule in each locule. The combination of laticiferous elements in leaves and stems and of two-armed hairs (one arm of which is sometimes suppressed) characterizes the family anatomically.

The delimitation of species and of genera, in particular, is difficult in the family, leading to both "splitting" and "lumping" at all taxonomic levels. After a period of neglect, a number of relatively recent studies have clarified the taxonomy and nomenclature of many groups, but it is likely that still further changes of both kinds will be made as the various groups become better understood. Taxonomic characters of generic significance have included especially the presence or absence of staminodia and endosperm, the presence or absence and location of appendages on the corolla lobes, and the general type of seed-scar (hilum).

Unfortunately, very few observations seem to have been made on the biology of the group, and little is known concerning the functioning of staminodia and petal appendages in connection with pollination.

The family is the source of a number of economically important timbers; the seeds of several genera provide edible oils; and a number of groups are valued for the refractive rubbery compounds from the coagulated latex (gutta-percha from species of *Palaquium*, *Payena*, and *Mimusops*; chicle from *Manilkara Zapota* and related plants; balata from *Manilkara bidentata* and related species). The family is also well known for a number of excellent tropical dessert fruits (most of which become quite rubbery and inedible when cooked), including the sapodilla (*Manilkara Zapota*), the sapote or marmalade plum (*Pouteria mammosa* (L.) Cronq., *Calocarpum Sapota* (Jacq.) Merr.), the eggfruit or canistel (*Pouteria campechiana*), and the star apple (*Chrysophyllum Cainito*).

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KEY TO THE GENERA OF SAPOTACEAE

- A. Sepals imbricate or spiraled, not distinctly biseriate, 4-9, commonly 5, or sometimes in *Pouteria* decussate (2+2) when 4; flowers solitary in the axils or several to many in axillary clusters.
- B. Staminodia present, scale-like or petaloid, secondary lateral leaf-veins reticulate, not parallel to the primary ones; leaves glabrous or variously pubescent beneath (only in *Bumelia* sometimes rufous-sericeous).
- C. Flowers numerous in axillary clusters, small, the sepals 1-3.5 mm. long, the corolla 3-5 mm. long; hilum small, basilateral.
- D. Corolla-lobes without lateral lobes; ovary essentially glabrous; mature fruits 1.5-3 cm. long; endosperm present. 1. *Mastichodendron*.
- D. Corolla-lobes with lateral lobes; ovary hairy or glabrous; mature fruits 6-12 mm. long.
- E. Plants unarmed; sepals pubescent; ovary glabrous (rarely slightly hairy); young and mature fruits commonly abruptly tapering into the style; endosperm present; cotyledons thin. 2. *Dipholis*.
- E. Plants usually more or less spiny; sepals glabrous or pubescent; ovary usually hairy; young and mature fruits commonly broadly rounded to subtruncate or retuse at the apex; endosperm wanting; cotyledons fleshy. 3. *Bumelia*.
- C. Flowers solitary or generally clustered in the axils, relatively large, the sepals 4-9 mm. long, the corolla 8-16 mm. long; hilum long, lateral; endosperm wanting; ovary hairy. 5. *Pouteria*.
- B. Staminodia absent; secondary lateral leaf-veins (seen from lower surface after removal of trichomes) parallel to the primary ones; leaves densely rufous-sericeous beneath; flowers 4-7 mm. long; ovary hairy; endosperm present. 4. *Chrysophyllum*.
- A. Sepals in 2 distinct series, 6 (3+3), or occasionally 8 (4+4); flowers solitary or 2 or 3 together in the axils, relatively large, the sepals 4-10 mm. long, the corolla 4.5-13 mm. long; staminodia present, petaloid to fleshy, or sometimes nearly obsolete; hilum lateral; endosperm present. 6. *Manilkara*.

Subfam. SIDEROXYLOIDEAE Lam

1. *Mastichodendron* Cronquist, Lloydia 9: 245. 1946.

Evergreen shrubs or trees with alternate or subopposite leaves, the midrib elevated on the lower leaf-surface, canaliculate above and often ending in a conical pouch at the summit of the long petiole, the blade pinnately open-reticulate veined, not closely areolate. Flowers numerous in axillary clusters. Sepals 5, suborbicular, spirally arranged. Corolla 5-lobed, firm-

textured, subrotate, the tube short, the lobes imbricate. Stamens 5, adnate to the corolla-lobes at or near the level of the sinuses; staminodia 5, not petaloid, shorter than the corolla-lobes. Ovary essentially glabrous, the locules usually 5, the ovules attached basilaterally. Fruit more or less fleshy, 1.5–3[–4.5] cm. long. Seed usually solitary, 1–2.5 cm. long, the hilum lanceolate to circular, to 9 mm. long, but not extending to the middle of the seed; embryo erect; endosperm abundant. (*Sideroxylon* sensu Dubard, Small, not L.) TYPE SPECIES: *Sideroxylon foetidissimum* Jacq. = *Mastichodendron foetidissimum* (Jacq.) Cronq. (The name from Greek, *mastico*, to chew, and *dendron*, tree, presumably alluding to chicle, the coagulated latex used as a base in the manufacture of chewing gum, obtained commercially from *Manilkara Zapota*.) — MASTIC, WILD-OLIVE.

As presently defined, a genus of about seven species of Florida, the West Indies, Mexico, and Central America; represented in our area by a single species in southern Florida.

Mastichodendron foetidissimum is an evergreen tree to 25 m. tall with long-petioled, yellow-green leaves with ovate to elliptic blades, glossy on both surfaces, the margins characteristically minutely puckered. The small, yellowish flowers appear throughout the year and are followed by one-seeded, juicy, yellow fruits 1.5–3 cm. long. The strong, dense, orange-colored heart-wood is sometimes used locally in cabinet-work and boat-building. Varietas *foetidissimum*, with broadly elliptic to suborbicular seed-scars mostly less than 4 mm. long, has a wide distribution from southern Florida through the West Indies from the Bahamas to Guadeloupe and Martinique. It occurs in the coastal hammocks of Florida as far north as Brevard County. Varietas *Gaumeri* (Pittier) Cronq., with larger, lanceolate or narrowly elliptic seed-scars, is known from British Honduras and Campeche and Yucatán, Mexico.

Dubard segregated the American species comprising *Mastichodendron* from the African *Sideroxylon* L. (type species, *S. inerme* L.) on the basis of the vertical (rather than horizontal) embryo and the open-reticulate (rather than closely areolate) venation of the leaf. However, he mistakenly applied *Sideroxylon* to the American species, treating the African as *Calvaria* Commers.; *Mastichodendron* is a renaming of the American group. *Mastichodendron* is considered by Cronquist to be the least specialized of the American genera.

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2. *Dipholis* A. de Candolle, Prodr. 8: 188. 1844, nom. cons.

Unarmed shrubs or trees with pinnately veined leaves, the primary lateral veins not very numerous, sometimes obscure. Flowers of ours numerous in axillary clusters. Sepals (4–)5[–9], pubescent, obtuse. Corolla-lobes 5, rarely 6, obtuse, about as long as the tube, each lobe always with a pair of

acute lateral lobes or appendages at the base. Stamens as many as the corolla-lobes, the filaments adnate at or near the level of the sinuses. Staminodia petaloid, erose-fimbriate-laciniate, alternate with the lobes of the corolla and attached at or near the level of the sinuses. Ovary nearly always glabrous, rarely with short, appressed pubescence, 5-locular, the ovules attached basi-laterally. Fruit tapering abruptly into the short, persistent style, fleshy and to 1[-3] cm. long at maturity, black in ours, mostly 1-seeded. Seed with a very nearly basal [or rarely basilateral] hilum, the endosperm well developed, the cotyledons thin. (*Spondogona* Raf., 1836, nom. rejic.) TYPE SPECIES: *Dipholis salicifolia* (L.) A. DC. (The name from Greek, *di*, two, and *pholis*, scale, alluding to the paired corolla-lobe appendages.)

About 14 species, confined to tropical North America, with the principal concentration of species in the Greater Antilles (10 species), only one reaching southern Florida.

Dipholis salicifolia, busic or cassada, of wide distribution, occurs in the hammocks of the Everglade Keys and the Florida Keys, in the Bahamas, southward through the West Indies to Guadeloupe and Barbados, and in southern Mexico, British Honduras, and Guatemala. It is a large shrub or tree (to 25 m.), evergreen, with elliptic to elliptic-lanceolate or -oblanceolate leaves, acute or acuminate at both ends. The numerous, small, white, fragrant flowers, borne more or less continuously throughout the year in simple, globose clusters at defoliated nodes or in leaf axils are followed by broadly ellipsoid or subglobose black fruits, 6-10 mm. long, containing one (or sometimes two or three) seeds. The very dense, red or dark-brown wood is sometimes used locally in cabinet work.

Similar to and perhaps derived from *Mastichodendron*, *Dipholis* differs from that genus primarily in the presence of lateral lobes on the corolla-segments. It is also closely related to *Bumelia* (see below).

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3. *Bumelia* Swartz, Prodr. Veg. Ind. Occ. 49. 1788, nom. cons.

Trees or shrubs, commonly but not always armed with spines or thorns, and with very tough wood. Leaves alternate or subopposite, generally small, the primary lateral veins not numerous, sometimes obscure, our species mostly with conspicuously reticulate-veiny leaves. Flowers 5 (rarely 4 or 6)-merous throughout, 3-numerous in axillary clusters, proterogynous. Sepals glabrous or pubescent, oval or orbicular, obtuse. Corolla-lobes each with a pair of lateral lobes or appendages at the base [or these sometimes wanting]. Stamens epipetalous, opposite the corolla-lobes, the anthers extrorse, the filaments slender. Staminodia petaloid, entire, erose or laciniate, attached to the corolla alternate with the stamens at or near the level of the

sinuses. Ovary usually hairy, sometimes glabrous, the ovules usually 5, attached basilaterally. Fruit generally broadly rounded, subtruncate or retuse at the apex, 1-seeded, fleshy at maturity, purplish black, and not over about 1.5[–2.5] cm. in length. Seed with a small, nearly basal hilum, without endosperm, the cotyledons fleshy. (? *Robertia* Scop. 1777, nom. rejic.) TYPE SPECIES: *Bumelia retusa* Sw. (The name ancient Greek for a kind of ash-tree.) — BUCKTHORN, IRONWOOD.



FIG. 1. *Bumelia*. a–g, *B. lanuginosa* subsp. *lanuginosa*: a, flowering branchlet, $\times \frac{1}{2}$; b, flower, $\times 6$; c, opened corolla, from without, two petals turned down to show lateral appendages and stamens, $\times 6$; d, opened corolla from within, two staminodia turned down to show lateral appendages of petals, one staminodium removed, anthers drawn as though erect (cf. b), $\times 6$; e, single petal with appendages and stamen from within, $\times 6$; f, gynoecium, with ovary in vertical section to show ovule, $\times 10$; g, cross section of ovary above point of attachment of ovules to show five ovules and incomplete septation of ovary (semidiagrammatic), $\times 15$. h, i, *B. celastrina*: h, tip of fruiting branchlet, $\times \frac{1}{2}$; i, seed, lateral view, $\times 2$.

About 25 species, chiefly of the warm regions of North America, a few species in South America, reaching northern Argentina. The genus is well developed in both continental and Caribbean North America. About six species occur in our area.

A number of the species of *Bumelia* are widespread and variable. Specific lines are difficult to determine, and constant morphological characters are few in number. Pedicel-length, used in the past as a basis for specific distinctions, is extremely variable and unreliable. Form and color of pubescence are helpful in delimiting the entities, but considerable changes may accompany age, the young leaves and twigs being quite different in appearance from the mature ones. Clark recognized 12 species in the southeastern United States; Cronquist admitted only 6 from the same area, but

included essentially the same number of entities under a different hierarchical arrangement.

Five of the species of the southeastern United States have conspicuously reticulate leaves and short styles 0.8–2 mm. long. *Bumelia lanuginosa* (Michx.) Pers., of wide distribution (Florida to Missouri, Kansas, Texas, southern Arizona and northern Mexico), is a more or less thorny shrub or tree to 15 m. tall, with leaves loosely woolly-villous beneath and fruits 7–15 mm. long. Two of its three subspecies occur in our area: subsp. *lanuginosa* (*B. rufa* Raf.) with tawny pubescence, ranges almost entirely east of the Mississippi River, and subsp. *oblongifolia* (Nutt.) Cronq., with gray to almost white pubescence, almost entirely to the west. Subspecies *rigida* (Gray) Cronquist, with small leaves and a different altitudinal range occurs entirely to the west of our region. *Bumelia lycioides* (L.) Pers. (including var. *virginiana* Fern., *B. Smallii* Clark, *B. cassinifolia* Small, *B. lucida* Small), a shrub or small tree with leaves silvery strigose or sericeous beneath, but glabrate in age, and with fruits 7–13 mm. long, ranges from Florida north to southern Virginia, southern Indiana, southern Missouri and to Arkansas and eastern Texas. *Bumelia reclinata* (Michx.) Vent., with small leaves, hairy when young but soon glabrate, and with small fruits (4–7 mm. long), is restricted to Florida and southern Georgia. It consists of var. *reclinata* (including *B. microcarpa* Small), with whitish or grayish leaf-pubescence and sparsely hairy young twigs, and of var. *rufotomentosa* (Small) Cronq., with coarser, rufous leaf-pubescence and densely rufous-tomentose twigs, which is of local distribution from Alachua to Orange and Hillsborough counties, Florida. *Bumelia Thornei* Cronq., of Early, Baker, and Calhoun counties, Georgia, appears to combine the characters of *B. reclinata* and *B. lanuginosa*. *Bumelia tenax* (L.) Willd. (including *B. lacuum* Small, *B. megacocca* Small), a shrub or small tree with leaves densely sericeous or sericeous-tomentose beneath with tawny, rufous or white [*f. anomala* (Sarg.) Cronq.] hairs, is restricted to the Coastal Plain from South Carolina to Florida.

The sixth species, *Bumelia celastrina* HBK. (*B. angustifolia* Nutt.), is characterized by small, fascicled, inconspicuously reticulate leaves, by twigs, leaves, pedicels and sepals glabrous from the outset, by styles about 2.5–4 mm. long, and by fruits 7–13 mm. long. It occurs in the Bahamas, central Cuba, and southern Florida, northward along the coasts to Brevard and Levy counties, and from southern Texas southward through Central America to Venezuela.

Cronquist suggests that *Bumelia persimilis* Hemsl. (Mexico to Venezuela) is the most primitive species of the genus and that evolutionary trends are toward reduction in size of plant, in size of leaves and prominence of reticulation, in size of fruits, and sometimes in number of flowers in a cluster.

Bumelia differs from *Dipholis* primarily by the possession of endosperm. The presence or absence of endosperm (admittedly difficult to determine in herbarium specimens) apparently parallels natural groupings on other bases, so that the genera usually may be distinguished without resort to this character. In *Bumelia* the plants are commonly spiny or thorny, the lat-

eral appendages of the corolla-lobes wanting (although present in our species), the ovary usually hairy (or only occasionally glabrous), the young as well as the mature fruits broadly rounded to subtruncate or even retuse at the apex, and the cotyledons fleshy. In *Dipholis*, by contrast, the plants are unarmed, the lateral appendages of the corolla-lobes always present, the ovary nearly always glabrous, the fruits tapering abruptly into the style, the cotyledons thin. Preliminary studies of woods also appear to justify separation of the two genera (Record, 1939).

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4. *Chrysophyllum* Linnaeus, *Sp. Pl.* 1: 192. 1753; *Gen. Pl.* ed. 5. 88. 1754.

Evergreen shrubs or trees with alternate, short-petioled leaves, ours smooth, shining above, satiny beneath with lustrous golden to brown hairs, the secondary lateral veins parallel to the primary, and the long axes of the areolae more or less parallel to the lateral veins. Flowers few to many in axillary clusters, or occasionally solitary. Sepals 5, in ours not over 3 mm. long, broader than long, obtuse. Corolla not over 6 mm. long, campanulate-cylindric, the lobes 5[4-11], the tube about as long as the lobes. Stamens 5[-10], adnate to the corolla at or near the level of the sinuses, the anthers extrorse; staminodia none (or occasionally in individual flowers 1 or more irregularly developed in the corolla-sinuses). Ovary surmounted by a short, columnar style and a 5[-7-12]-lobed stigma; ovules attached laterally or basilaterally. Seeds 1, or sometimes several, the seed-scar 5 mm. or more in length, broadly elliptic to subcordate [or narrow or covering nearly the whole surface of the seed]; endosperm abundant. TYPE SPECIES: *Chrysophyllum Cainito* L. (The name from Greek, *chrysos*, gold, and *phyllon*, leaf, in reference to the hairs on the lower leaf-surfaces.) — GOLDEN-LEAF, SATIN-LEAF.

About 11 species in tropical North America, 30 in South America, 15 in tropical West Africa, and 25 in Australasia (16 in New Caledonia); a single species indigenous in subtropical Florida.

Chrysophyllum oliviforme L., satin-leaf, is an evergreen shrub or small tree with an upright plume-like crown of dark green, smooth and shining, ovate leaves, the under surfaces densely covered with lustrous, copper-colored hairs. The small, white flowers, produced irregularly throughout the year, are followed by olive-like dark purple one-seeded fruits. The hard, close-grained, light brown wood is sometimes used locally in cabinet-work. Varietas *oliviforme* ($2n = 52$), with leaves more than 5 cm. long and several to many flowers in a cluster, is occasional in thickets and coastal hammocks of southern peninsular Florida and the Keys, northward to Brevard and Lee counties, and is common in the Bahamas and the Greater Antilles. Varietas *picardae* (Urb.) Cronq., characterized by smaller leaves and fewer flowers per cluster, is known from a few collections from Hispaniola.

Chrysophyllum Cainito, the star apple ($2n = 26$), a handsome tree grown for its excellent fruit, is frequent in cultivation in southern Florida.

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5. *Pouteria* Aublet, Hist. Pl. Guiane Franç. **1**: 85. *pl.* 33. 1775.

Trees or shrubs with alternate, occasionally subopposite leaves, the primary lateral veins strongly arcuate near the margin, scarcely crowded. Flowers solitary or generally several in axillary clusters. Sepals 4-6[-12], distinct, decussate when 4, otherwise imbricate, in ours 4-9 mm. long. Corolla white to yellow or green, subrotate to cylindric, 4-7 (commonly 5 or 6)-lobed, the inner lobes sometimes larger than the outer, shorter than the tube, papillate or sericeous outside. Stamens epipetalous, attached at or near the level of the sinuses [or at the base of the corolla], sometimes abortive. Staminodia alternate with the corolla-lobes and sometimes apparently in the same series [sometimes petaloid, rarely absent]. Ovary hairy, [1-]5-8[-10]-loculed, the ovules laterally attached. Fruit commonly fleshy, [sometimes sclerotic,] 1-several-seeded. Seeds with a long and often broad lateral hilum (or sometimes nearly the whole surface more or less grown to the pericarp); embryo with thick cotyledons; endosperm a thin layer or lacking. (*Lucuma* Mol., sensu many authors.) TYPE SPECIES: *Pouteria guianensis* Aubl. (The name derived from *pourouma-pouteri*, the Carib vernacular name of the type species.)

A genus of about 150 species, the largest number in tropical America,

with a number of species in Africa and in Australasia (about 28 species); representatives of two species in subtropical Florida.

Pouteria dominigensis (Gaertn. f.) Baehni is a small tree to 10 m. tall, with oblanceolate to obovate or elliptic leaves, and with evidently pedicellate yellow or white flowers (6–16 mm. long) either solitary or borne few together in the leaf-axils. The yellow, fleshy, edible fruits are 3–6 cm. in thickness and bear one to several seeds. Varietas *dominigensis*, with leaves essentially glabrous (except when very young) is distributed in Hispaniola, Cuba, the Bahamas, and subtropical Florida (where it apparently is rare). Varietas *cuprea* (Urb. & Ekm.) Cronq., differing in strongly rufous-strigose and only tardily glabrate leaf surfaces, is confined to Hispaniola.

The eggfruit or canistel, *Pouteria campechiana* (HBK.) Baehni, long known as *Lucuma nervosa* A. DC., is native from southern Mexico to Panama. It occurs in the hammocks of the Florida Keys and also in Cuba, either in cultivation or perhaps as a recent escape. A tree which sometimes attains a height of 25 m., this species has elliptic to narrowly obovate, glabrous leaves, rounded to acuminate at the apex, up to 35 mm. long and 10 cm. wide, and borne on petioles up to 4 cm. long. The flowers are clustered in the axils on pedicels about 1 cm. long and the subglobose or pyriform fruits, up to 7 cm. in diameter, are yellow, green or brownish with yellow or orange pulp with the consistency of hard-boiled egg-yolk. The species shows variation in size and shape of leaves, size and number of flower parts, and size and texture of fruits. Some of the numerous segregates which have been proposed may represent geographical varieties, but the final evaluation of these should be preceded by extensive field study.

Pouteria belongs to a complex about which there is little agreement as to generic lines. As currently treated, the group includes such generic segregates as *Calocarpum* Pierre and *Oxythece* Miq., but excludes as separate genera the New World *Micropholis* Pierre and the predominantly Australasian *Planchonella* Pierre.

Aublet's *Pouteria* was based upon a mixture of two discordant elements, for the fruit described and figured with the other parts of the plant is that of a species of *Sloanea* (Elaeocarpaceae). (See Radlkofer.) Although the name might be regarded as a *nomen confusum*, Radlkofer, after reviewing the situation, re-established *Pouteria* for that part of the type belonging to the Sapotaceae. In the past *Lucuma* Mol. (1782) has been applied to the species here considered as *Pouteria*. However, three of the five species originally described by Molina generally are agreed not to be sapotaceous, and, although the identity of the others is uncertain, the description is such that these, too, may be excluded from the Sapotaceae.

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Subfam. MIMUSOPOIDEAE Lam

6. **Manilkara** Adanson, Fam. Pl. 2: 166. 1763, nom. cons.²

Evergreen trees or shrubs with alternate, leathery leaves often approximate or clustered at the ends of the stout branchlets, the primary lateral veins generally parallel, nearly straight, not crowded. Flowers of our species on pendent pedicels, solitary or 2 or 3 together in the leaf-axils. Sepals biseriate, 3 + 3 [rarely 2 + 2 or 4 + 4], persistent, reflexed in age. Corolla white or yellow, glabrous, the lobes as many as the sepals, each with a pair of petaloid dorsal appendages or these obsolete by fusion with the lobes. Stamens as many as corolla lobes and opposite them, epipetalous, the anthers sagittate; staminodia of the same number as stamens and alternating with them, petaloid to fleshy (or almost obsolete). Style linear, exerted; stigma entire; ovary ovoid to depressed globose, pubescent, 6–14-locular (in ours 9–12- or 6-locular), the ovules lateral in attachment. Fruit ellipsoid, ovoid to depressed globose, fleshy, 1- or several-seeded, capped by the persistent style. Seed with a long, lateral hilum; embryo with thin cotyledons; endosperm abundant. (*Mimusops* sensu Sargent, Small and others, in respect to American species; including *Achras* L., *Sapota* Mill., nom. rejic.) TYPE SPECIES: *Manilkara Kauki* (L.) Dubard (*Mimusops Kauki* L.). (The name from Malabar, *manyl-kara*, as given by Rheede in *Hortus Malabaricus*, applied to a species of this genus.)

A genus of about 85 species in four subgenera, in the tropics of both hemispheres (about 30 in Africa, 25 in Australasia, and 30 in the Caribbean, Central America and South America); two species, one native, the other introduced, in subtropical Florida.

Manilkara bahamensis (Baker) Lam & Meeuse (*Achras emarginata* (L.) Little, *Minusops emarginata* (L.) Britton), wild dilly or wild sapodilla, of the Florida Keys and the Bahamas, is an evergreen shrub or small tree with bluish-green, coriaceous, elliptic, blunt or emarginate, petiolate leaves

² Both *Achras* L. and *Manilkara* Adans. have been proposed for conservation. (See Little, Brittonia 7: 48, 49. 1949, and Lam and Van Royen, Taxon 2: 112. 1953, respectively.) The former has been rejected (Taxon 3: 119. 1954), while the latter has been approved by the Committee for Spermatophyta.

clustered at the ends of the stout branchlets. The small, yellowish flowers on recurved pedicels are borne singly or in two's or three's in the leaf-axils in April or May. The subglobose, fleshy, one-seeded, rusty-brown, mealy-roughened fruits reach 3 cm. or more in diameter. This taxon has been treated either as a species or, in the rather broad specific concept of Cronquist, as one of four subspecies of *Manilkara jaimiqui* (Wright) Dubard.

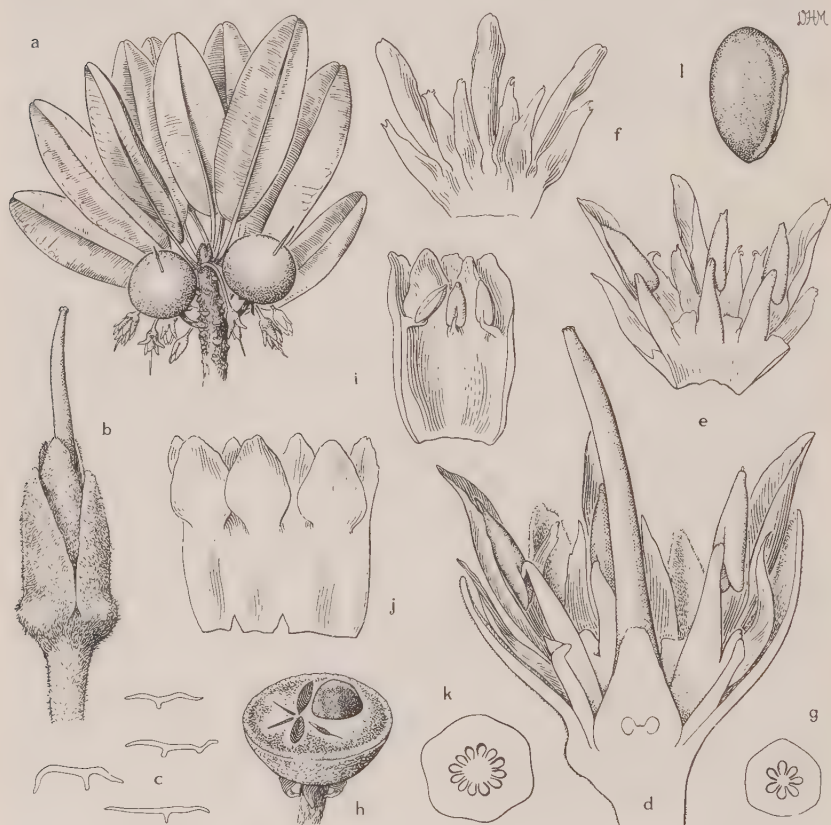


FIG. 2. *Manilkara*. a-h, *M. bahamensis*: a, tip of flowering and fruiting branch, $\times \frac{1}{2}$; b, flower, lateral view, after fall of corolla, $\times 3$; c, detached two-armed hairs from calyx, point of attachment below, $\times 50$; d, flower in vertical section, outer sepal to the left — note staminodia alternating with stamens, $\times 5$; e, three corolla-lobes, from within, with appendages, stamens, alternating staminodia, $\times 3$; f, three corolla-lobes, from without, to show dorsal appendages (cf. Fig. 1c, $\times 3$; g, cross section of 7-locular ovary at level of attachment of ovules (semidiagrammatic), $\times 5$; h, nearly mature fruit, the upper half removed, to show single seed, locules with aborted ovules, $\times 1$. i-l, *M. Zapota*: i, portion of corolla, from within, to show three corolla-lobes, two petaloid staminodia alternate with stamens, $\times 3$; j, portion of corolla, from without, to show three corolla-lobes, tips of four staminodia, $\times 3$; k, cross section of 12-locular ovary at level of attachment of ovules (semidiagrammatic), $\times 5$; l, seed, lateral view — note elongate seed-scar, $\times 1$.

Our plant is subsp. *emarginata* (L.) Cronq.; the others are subsp. *jaimiqui* and *Wrightiana* (Pierre) Cronq., of Cuba, and subsp. *haitiensis* (Cronq.) Cronq., of Hispaniola.

Manilkara Zapota (L.) v. Royen (*M. Zapotilla* (Jacq.) Gilly, *Achras Zapota* L.), sapodilla, dilly, or naseberry, $2n = 26$, is cultivated in most of the warmer regions of the world for its excellent fruits. In its native area (Mexico to Costa Rica), especially in Yucatán, northern British Honduras, and Petén, Guatemala, it is also the principal source of chicle for chewing gum. The plant is a handsome evergreen tree with small, white flowers borne singly in the leaf-axils and followed by globose to ellipsoid fruits 3–9 cm. in diameter with translucent, pale brown flesh and several shining, black, compressed seeds. It is quite hardy in southern Florida, and outside of cultivation occurs in hammocks and old fields on the Everglade Keys and Florida Keys.

These two species would be placed respectively with *Manilkara* Adans. and *Achras* L., which, although similar in most respects, have been maintained as separate genera on the basis of the lack of paired dorsal appendages on the petals of the latter. However, the two genera were combined by Gilly who found transitional forms in his study of the *M. Zapota* complex. This union has been accepted generally, but the correct name for the genus so constituted has been a matter of controversy which is only settled by the conservation of *Manilkara* and the rejection of *Achras*.

A segregate of *Mimusops* L. (a group of about 60 species, mostly African), *Manilkara* is usually distinguished from that genus by sepal-number (6 *vs.* 8) and corresponding differences in the number of corolla-lobes, stamens and staminodia, by the seed-scars (relatively long and lateral *vs.* small and basilateral), by the nervation of the leaves (generally straight, parallel, and rather close *vs.* curved, wider apart), by the presence or absence of sclereids in the leaves (according to Lecomte — on the basis of only eight species), by the locules of the ovary (15–6 *vs.* 8), by the embryo (with thin, foliaceous *vs.* thick, plano-convex cotyledons), and by the presence or absence of endosperm. Although most workers at present recognize the two as distinct, a few species appear to be intermediate. On the basis of a preliminary study of Sapotaceous woods, Record thought that both might be included in a single genus.

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EBENACEAE (EBONY FAMILY)

Monoecious, dioecious, or polygamous trees or shrubs with alternate [rarely opposite], simple, entire, exstipulate leaves and watery sap; nodes with 1 trace from 1 gap. Flowers regular, 3-7-merous, sympetalous. Stamens epipetalous or hypogynous, 2-4 times as many as and opposite the lobes of the corolla. Gynoecium syncarpous, the styles wholly or partly distinct, the 2-16(-20)-locular ovary superior, with 1 (or 2) bitegumented ovules suspended from the summit of each locule. Fruit a berry. (Ebenaceae Vent. Tab. Regne Vég. 2: 443. 1799, nom. cons. prop. [Type genus: *Diospyros* L. (*Ebenus* Burm. ex Ktze., not L.; *Maba* J. R. & G. Forster)]; *Guaia-canae* Juss. Gen. Pl. 155. 1789, nom. illegit. [Type genus: *Diospyros* L. (*Guaia-cana* Tourn., not *Guaia-cum* L.)].)³

A small, geologically old family, well represented in the fossil record, including four or five weakly defined genera (all except *Diospyros* confined to Africa or Madagascar) and about 450 living species, almost all restricted to tropical regions of both Eastern and Western hemispheres, with the greatest concentration of species in India and Malaysia, several in subtropical regions, a few species in the temperate regions of Asia and America, and none in the colder parts of either hemisphere.

The watery sap, usually unisexual flowers, and 2-integumented, pendulous ovules distinguish the Ebenaceae from the Sapotaceae which have milky sap, usually bisexual flowers, and 1-integumented, ascending ovules. The Styracaceae, with which the Ebenaceae are also thought to be allied, have bisexual flowers and an incompletely septate ovary (usually), which may be superior, half-inferior or inferior. Metcalfe and Chalk note a close general similarity between the woods of Sapotaceae and Ebenaceae, and Erdtman indicates that pollen grains more or less similar to those of Ebenaceae are found in the Sapotaceae and Styracaceae. The hairs of

³ The well-known and long-used name Ebenaceae must be conserved, for it is derived not from that of a genus but from ebony, the wood of *Diospyros Ebenum*. (In establishing the family Ventenat wrote, "Les rapports que les plantes de cette famille ont avec l'arbre qui produit la véritable ébène, nous ont déterminés à leur donner le nom d'Ébénacées.") Linnaeus used *Ebenus* for a genus of Leguminosae, and the only post-Linnaean publication of the name in the sense of *Diospyros* (*Maba*) is that of Otto Kuntze, Rev. Gen. 2: 408, 1891. Bullock (See Taxon 7: 14, 17, 160. 1958; 8: 170. 1959) has proposed conservation of Ebenaceae Vent. and rejection of *Guaia-canae* Juss. The former certainly must be conserved, but the latter is already illegitimate under the International Code of Botanical Nomenclature, being derived from *Guaia-cana* Tourn. (not *Guaia-cum* L., of the Zygophyllaceae), which does not seem to have been published as a generic name after 1754.

Ebenaceae are mostly unicellular, but are occasionally in tufts and sometimes are 2-armed.

The family is of economic importance for a number of woods, especially ebony, the hard and heavy, black heartwood of several Asiatic species of *Diospyros*, *D. Ebenum* Koenig being the classical source. Several species, mostly of *Diospyros* (see below), have edible fruits.

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1. *Diospyros* Linnaeus, Sp. Pl. 2: 1057. 1753; Gen. Pl. ed. 5. 478. 1754.

Dioecious (or rarely polygamous) trees (or shrubs) with dense, hard wood. Flowers greenish, axillary, cymose, or the pistillate (larger than the staminate) solitary. Calyx [3]4–6[7]-lobed, accrescent in fruit, coriaceous or foliaceous. Corolla urceolate-campanulate with [3]4–6 lobes sinistrorsely contorted in the bud, spreading or recurved at anthesis, the tube usually contracted at the top. Stamens 3–many, usually in two or more rows, unequal, often in pairs, in ours mostly 16 in the staminate flowers (8 imperfect rudimentary ones in the pistillate or these sometimes absent), the filaments short, hairy [or glabrous], the anthers linear-lanceolate, arched inward, apiculate by the excurrent connective, 2-loculed, dehiscing laterally by longitudinal slits. Pollen 3-colporate. Styles usually 4, united below; stigmas emarginate or punctiform; ovary (rudimentary or absent in the staminate flowers) usually 8-locular [3 or 6, or 4 or 8–16-locular in other species], the ovules solitary [or 2] in each locule. Berry depressed-globose, globose, oblong or conical, sessile or subsessile, pruinose, bitter-astringent when green, orange, sweet, and soft-pulpy when ripe. Seed oblong, the testa brown, more or less shining, the endosperm cartilaginous, equable [or in some species ruminated by sinuous intrusions of the testa.] Embryo straight, the contiguous cotyledons foliaceous. Embryo sac development of the "Polygonum" type, seedless fruits sometimes developing. (Including *Maba* J. R. & G. Forster, *Brayodendron* Small.) TYPE SPECIES: *D. Lotus* L. (The name from Greek, *Dios*, of Zeus (genitive), and *pyros*, grain; used by Theophrastus for a fruit, adopted by Linnaeus in preference to *Guaiacana* Tourn., which was not of Greek or Latin derivation.) — PER-SIMMON, DATE-PLUM.

A large genus of about 400 species of tropical and warm regions (including about 175 in Malaysia, 70 in Africa, 100 in Madagascar); only a few reaching into the temperate climates of North America and Asia; two species indigenous to the United States: *D. texana* Scheele, of southwestern Texas and northern Mexico (segregated on totally inadequate grounds as *Brayodendron* Small), and *D. virginiana* L., in the eastern United States.

Diospyros virginiana, persimmon, simmon, possumwood, a deciduous tree, usually 10–15 m. tall, with heavy, hard wood, ranges from Texas to Florida and northward to Connecticut and southeastern Iowa, but is uncommon in the area of the Wisconsin glaciation. Although the genus is known from the fossil record to have been distributed at one time far to the north, the present range of this species appears to be limited by temperature and rainfall, few specimens being found north of the 25° F. February isotherm or west of the 30-inch isohyet.

Phenotypically variable, *Diospyros virginiana* has received various taxonomic treatments and is in need of further study. Varietas *pubescens* (Pursh) Dippel (Florida to Arkansas, north to Virginia, southern Illinois, and southern Iowa) is characterized by villous or densely tomentose branchlets and leaves pubescent beneath. The form known as var. *platycarpa* Sarg. (Missouri, Arkansas, Kansas and Oklahoma) has broad, depressed fruits which ripen early, and var. *Mosieri* (Small) Sarg. (peninsular Florida) is said to be a shrub or small tree distinguished by thick-skinned, globose fruits and plump, slightly rugose seeds. Fruit-size and -shape are quite variable in this species and merit careful taxonomic attention. (See also references to *D. Kaki* below.)

The basic chromosome number of the genus appears to be 15, $2n$ having been reported as 30 for *Diospyros texana* and four exotic species (including *D. Lotus*), 60 (tetraploid) and 90 (hexaploid) for *D. virginiana*, and 90 for *D. Kaki* L. f. In *D. virginiana* the tetraploids occupy the central and southeastern parts of the range of the species, with the hexaploids on the periphery throughout. Morphological variation, as well as variation with respect to hardiness in this species, may be related to polyploidy. Sometimes used as a stock upon which *D. Kaki* is grafted, it provides ideal material for the study of stock–scion relationships with respect to ploidy.

Diospyros virginiana is self-pruning (as in species of *Salix*, *Populus*, *Ulmus* and *Quercus*), some of the twigs abscising after the first year, most after the second, and some during successive years, while only relatively few are retained and become the stark, secondary branches of the tree. Root suckers are readily produced and clonal stands are frequent, especially in old fields.

Although the flowers are visited by bees in large numbers, the occasional development of seedless fruits (cf. *Diospyros Kaki*) has led to speculation concerning the necessity of fertilization for the production of the normal, seed-bearing fruits. There are, however, indications that pollination is necessary for ordinary fruit production and that fertilization does occur, although this latter process has not been observed.

Dormancy of the seeds is due, in part, to the mechanical resistance of the

seed coat, particularly the layer overlying the radicle. The physiological effects upon germination of the passage of the seeds through the alimentary tract of animals — such as foxes, deer, raccoons, and opossums — which feed upon the fruits, and the role of such animals in the spread of the species are not known.

A number of selections of *Diospyros virginiana* have been named, and the species is cultivated to a limited degree, although seldom on a commercial scale. Chinese and Japanese cultivars of *D. Kaki*, with large and delicious fruits, are cultivated commercially in northern Florida and California and are grown for ornament and fruit over much of our area. The numerous studies of *D. Kaki* suggest profitable lines of investigation on *D. virginiana*.

The closest relative of *Diospyros virginiana* appears to be *D. Lotus*, which, with *D. Kaki*, *D. Morrisoniana* Walp., *D. glaucifolia* Metc., *D. brideliifolia* Elmer, and, probably, *D. blepharophylla* Standl. (*D. ciliata* A. DC.), *D. ehretioides* G. Don, and *D. mollis* Steud. (according to Bakhuizen van den Brink), constitutes section DIOSPYROS (sect. *Lotus* Bakh.; sect. *Danzleria* (Bert.) Hiern, in part). The studies of the Malaysian species by Bakhuizen van den Brink and of the African by White have clarified many of the specific problems for those areas, but White has pointed out that the entire subgeneric classification needs a complete overhaul which must await careful study of all of the species. Among the African members White has noted well-marked, isolated species and a number of "superspecies" consisting of two to five closely related geographically or ecologically vicarious species. Standley, Bakhuizen van den Brink, and White have all found it impossible to maintain *Maba* as distinct from *Diospyros*.

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STYRACACEAE (STYRAX FAMILY) ⁴

Shrubs or trees, usually more or less pubescent with stellate hairs [or peltate scales]. Leaves alternate, exstipulate, simple, entire, serrate or dentate, pinnately veined, the nodes with 1 trace from 1 gap. Flowers bisexual, in variously modified, basically cymose, terminal and axillary inflorescences (sometimes reduced to single axillary flowers). Calyx synsepalous, with 4 or 5 small teeth or lobes (or these obsolete), free from the ovary to completely adnate to it. Corolla sympetalous, usually 4- or 5-lobed [some-

⁴ By C. E. Wood, Jr.

times more], valvate or imbricate in aestivation. Stamens usually twice (to 4 times) as many as the corolla lobes, inserted in a single series on the base of the corolla, the filaments usually more or less connate at the base, free above, usually continuous with the connective, the anthers oblong, 4-locular; pollen 3-colporate, usually suboblate. Gynoecium syncarpous, the ovary superior to inferior, (2)3-5-locular or 1-locular above by failure of union of the septa; style usually filiform; stigma terminal, usually minutely 3-5-lobed. Ovules 1-many in each locule, axile, anatropous, pendulous, or erect, 2-integumented, or 1-integumented (presumably by fusion of the two). Fruit typically dry, indehiscent or dehiscent; seeds 1 to several, the seed coat thin to indurate; embryo usually straight, with broad cotyledons, surrounded by fleshy endosperm.

A family of about 13 genera, all except *Styrax* small, including about 150 species, centering in eastern Asia, but with numerous species in the New World, none in Australia, one in the eastern Mediterranean region, and about three in Africa. The family exhibits the marked disjunctions indicative of an ancient group.

The Styracaceae are characterized by a series of characters which contrast markedly with those of the Symplocaceae (*q.v.*). They are distinguished from other sympetalous groups by the combination of watery sap; bisexual flowers with stamens at least twice as many as the petals and apparently in a single series; oblong to linear, basifixed anthers with longitudinal dehiscence; single, linear style; superior to inferior, 2-5-locular ovary; and usually dry, capsular to indehiscent fruit. Stellate pubescence is characteristic of the entire family, in contrast with the simple hairs of Symplocaceae, the two-armed hairs of Sapotaceae, and the several types found in the Ebenaceae. Erdtman notes that pollen more or less similar to that of Styracaceae is found in the Ebenaceae, and that at least slightly similar pollen occurs in the Cornaceae and Nyssaceae, while that of Symplocaceae is different.

The Styracaceae include a number of ornamental trees and shrubs (especially *Styrax* and *Halesia*). *Styrax officinale* formerly was the source of storax, a gummy resin used in incense, and from *S. Benzoin* is obtained benzoin, a resin which is secreted when the bark and wood of the tree are injured.

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1. *Styrax* Linnaeus, Sp. Pl. 1: 444. 1753; Gen. Pl. ed. 5. 203. 1754.

Deciduous [or evergreen] shrubs or trees with entire or slightly serrate or dentate leaves; nearly all parts more or less pubescent with stellate hairs (or rarely glabrous). Inflorescences terminal or axillary, basically cymose but appearing racemose, the axillary sometimes reduced to single flowers, as in *S. americanum*, thus giving the appearance of partly foliose racemes. Calyx synsepalous, cup-like, 5-toothed (or rarely 2- or 3-toothed) [or undulate or subentire]. Corolla 5 (rarely 6 or 7)-parted, always white, valvate, valvate-induplicate, or imbricate in aestivation, the tube (usually) much shorter than the lobes. Stamens 10 [8–18], adnate to the tube of the corolla in a ring [and monadelphous in a short tube], the filaments continuous with the connective, glabrous or pilose or densely pilose at the base. Gynoecium syncarpous; stigma small, minutely 3-lobed, terminal; style linear, with a canal; ovary partially adnate to the calyx [or rarely free], 3-locular at the base, 1-locular above (the 3 parietal septa united below but incompletely united above with the central placental mass); ovules axile, usually 4–6 in each locule, 2-integumented and with an obturator (a massive outgrowth of the placenta), one of the uppermost developing into a seed. Fruit globose or oblong, dry, loculicidally 3-valvate [or irregularly dehiscent or indehiscent]; seeds 1 or rarely 2, subglobose or ellipsoid, with a basilateral hilum, the testa hard, smooth [or crustaceous, wrinkled, papillate, or with stellate hairs]. TYPE SPECIES: *S. officinale* L. (The name Greek, *styrax*, the ancient name for storax, a fragrant resin formerly used in incense, and for the plant (*S. officinale*) from which it was obtained.⁵ — STORAX.

A genus of about 120 species, mostly tropical and subtropical, of eastern Asia southward to New Guinea (but absent from the Philippines and Ceylon), the eastern Mediterranean region (a single species), South America, the West Indies, and Central America; about six species in the United States, two in our area. Two sections were recognized by Perkins: *STYRAX* (*Eustyrax* Perk.), with ovary 16–24-ovulate, and *FOVEOLARIA* (Ruiz & Pavon) Perk., with ovary 3–5 ovulate (2 species, Cuba and Peru).

Styrax americanum Lam., with flowers solitary or in pairs in the axils of leaves and paired at the tips of short branches, partially imbricate to valvate-induplicate aestivation of the corolla-lobes, and leaves 2–10 cm. long,

⁵ Different authors have treated the genus as neuter, feminine, or masculine. *Styrax* is masculine in Latin. In Greek it is masculine, feminine, or neuter, depending upon its meaning: the spike at the lower end of a spear-shaft (m.), the shrub or tree from which storax was obtained (f.), or the resin storax (n.). Linnaeus took *Styrax* from the Greek (see "Critica Botanica") and treated it as neuter throughout his work. Although one would expect the word to be feminine, following the Greek gender for the plant, in this instance it should be argued that there was a choice. Under Recommendation 75A(1) of the International Code of Botanical Nomenclature, Linnaeus' consistent practice in this matter should be followed, whether or not he followed his own precepts.

is a frequent shrub of low, acid, mostly nonalluvial soils from southwestern Florida, northward on the Atlantic coastal plain to southeastern Virginia, into the mountains of northeastern Alabama, and in the Mississippi embayment to western Tennessee, western Kentucky, southern Illinois, Indiana and Ohio, southeastern Missouri, the southeastern half of Arkansas, and eastern Texas. Pubescence and seed- and fruit-size are variable within the species and should be studied in connection with the status of forma *pulverulentum* (Michx.) Perk. (var. *pulverulentum* (Michx.) Rehd.).



FIG. 3. *Styrax*. a-i, *S. americanum*: a, flowering twig, $\times \frac{1}{2}$; b, flower, $\times 3$; c, stellate hair from petal, $\times 50$; d, flower in vertical section, the distal portions of petals, stamens, and style removed — note partially inferior ovary, styler canal, large placenta, incomplete septation, $\times 5$; e, cross section of ovary through uppermost ovules to show incomplete septation (semidiagrammatic), $\times 8$; f, capsular fruit with single large seed, $\times 2$; g, h, seeds from two Florida collections — compare size, note prominent raphe and basal hilum, $\times 2$; i, embryo, $\times 3$.

Styrax grandifolium Ait., with larger, apparently terminal, mostly bracteate "racemes" (with as many as 20 flowers), imbricate aestivation, obovate leaves 5–20 cm. long, larger, somewhat more elongate fruits, and larger seeds, is a handsome shrub or small tree of woodlands, bluffs, and stream banks, ranging from northern Florida to Louisiana, northward to central Arkansas, northeastern Mississippi, western Tennessee (along the western edge of the Highland Rim), northern Alabama, northeastern Georgia, and through the piedmont and coastal plain of North Carolina to southern Virginia. Although the ranges overlap in large part, the two species seem to be completely isolated ecologically.

Section STYRAX was divided by Gürke and by Perkins into two series, *Valvatae* and *Imbricatae*, on the basis of aestivation of the corolla lobes. As Van Steenis has shown, however, imbrication may vary widely with respect to both the individual and species. (Cf. *S. americanum*.) Although both of our species were placed with the *Imbricatae* by Perkins, neither appears to be closely related to the other, and, with the exception of *S. glabrescens* Benth. (Hidalgo and Veracruz, Mexico, to Costa Rica), which

is close to *S. grandifolium*, the relatives of both are all species of eastern Asia. The chromosomes of *S. Obassia* Sieb. & Zucc. (related to *S. grandifolium*) have been reported as $2n = 16$, and those of *S. japonicum* Sieb. & Zucc. (close to *S. americanum*?) as $2n = 40$.

The embryology, morphology, and anatomy of *Styrax officinale* var. *californicum* (Torr.) Rehd. have been studied in some detail, and Van Steenis has pointed out numerous biological features of the species of the East Indies. Curious tubular galls of several characteristic shapes are produced on the Asiatic species by Aphidae of the genus *Astegopteryx*.

Six or more of the hardier species of *Styrax* are in cultivation in the United States for their showy white flowers.

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2. *Halesia* Ellis ex Linnaeus, *Syst. Nat.* ed. 10. 1044, 1369. 1759, nom. cons.

Deciduous shrubs or trees with membranaceous, serrulate leaves. Inflorescences reduced to clusters or irregular short racemes of 2-4 (-5) long-pedicelled, pendent flowers in the axils of scars of leaves of the preceding year. Flowers 4-merous, showy, produced in early spring. Calyx almost completely adnate to the ovary, 4-ribbed, with 4 small teeth at the summit, or these obsolete. Corolla white to pale pink, campanulate, 4-cleft or -lobed, imbricate in aestivation but open long before anthesis. Stamens 8-16, united for about $\frac{1}{3}$ their length and adnate to the lower part of the corolla; filaments straight, continuous with the connective; anthers oblong, slightly curved outward, introrse, dehiscing lengthwise. Style slender, linear, stigma minutely 4-lobed; ovary almost completely inferior, the sterile tip tapering into the style, 2- or 4-locular, each locule with four 1-integumented ovules attached near the middle of the axis, the 2 upper erect, the 2 lower pendulous. Ovary elongating greatly after anthesis; fruit dry, indehiscent, beaked and winged, with a hard, clavate-fusiform endocarp, a thin, corky mesocarp and 2 or 4 corky, longitudinal wings. Seeds 1-3, nearly cylindrical, against the wall of the endocarp, completely surrounded by a stony covering, the remaining cavity of the endocarp filled with corky tissue. (*Mohria* Britton, not Swartz; *Mohrodendron* Britton, *Carlomohria* Greene;

not *Halesia* P. Br., 1756, nom. rejic.) TYPE SPECIES: *H. carolina* L. (Named in honor of Stephen Hales, 1677–1761, author of “Vegetable Statics” in 1722.) — SILVERBELL-TREE, SNOWDROP-TREE.

Two to four species of the southeastern United States and one species of Chekiang and Kwantung, China.

The genus is in need of a careful revision with particular emphasis on populations and studies of fully developed flowers and mature fruits. Herbarium materials are not very satisfactory in this group, for corollas and green fruits shrink and become distorted in drying, and the wings of ripe fruits are corky and brittle. In addition, the corolla attains its general shape early and is quite open while still green and half-grown, continuing to enlarge until (? or after) anthesis, thus leading to erroneous comparisons of size. Pubescence may be ephemeral, and plants may begin to flower at an early age.

Halesia diptera Ellis is a well-defined species distributed across the southern Coastal Plain in a band roughly delimited by Chatham County, Georgia; Leon County, Florida; Elmore and Chilton counties, Alabama; Ouachita and Natchitoches parishes, Louisiana; and Sabine and Harris counties, Texas. The type material came from near Augusta, Richmond County, Georgia, and the species has been reported in the Georgia piedmont in Meriwether and Upson counties. The plant is a shrub or tree up to 10 m. tall, with elliptic to obovate, abruptly long-acuminate, remotely sinuate-serrulate leaves, tomentose calyx and pedicels, a deeply cleft corolla 1.5–3 cm. long, with a very short tube and oval to obovate lobes, 8 equal stamens, 2-locular ovary (rarely 4-locular), and a fruit with 2 broad wings. Fruit shape is variable, with the wings either rounded or tapered at the base. Two varieties have been distinguished: var. *magniflora* Godfrey, described as limited to mixed woodlands of upland slopes, river bluffs, and ravine slopes in the limited area from Leon to Jackson County, Florida, with corollas 2–3 cm. long and lobes 1–1.5 cm. broad; and var. *diptera*, inhabiting flood-plain forests of the Escambia and Choctawhatchee rivers of western Florida, and ranging westward and northeastward, with corollas 1–1.5 cm. long and lobes 0.8–1 cm. broad. Further study is needed, for, although plants to the west of Florida appear to be small flowered, the larger-flowered plant apparently occurs in southwestern Georgia and adjacent Alabama, and, in Chatham County, Georgia, the easternmost locality for the species, the flowers are as large as those from Leon County, Florida.

A second group is the *Halesia carolina* complex which is distributed primarily from western North Carolina and eastern Tennessee to the coastal plain of Georgia, northern Florida, Alabama, and Mississippi. The group extends northward across western Virginia into southern West Virginia along the New River drainage, and scattered stations occur along the Cumberland River drainage (Harlan County, Kentucky; Davidson County, Tennessee), along the Tennessee River (Lauderdale County, Alabama; Hardin and Decatur counties, Tennessee), and on the Ohio River near the

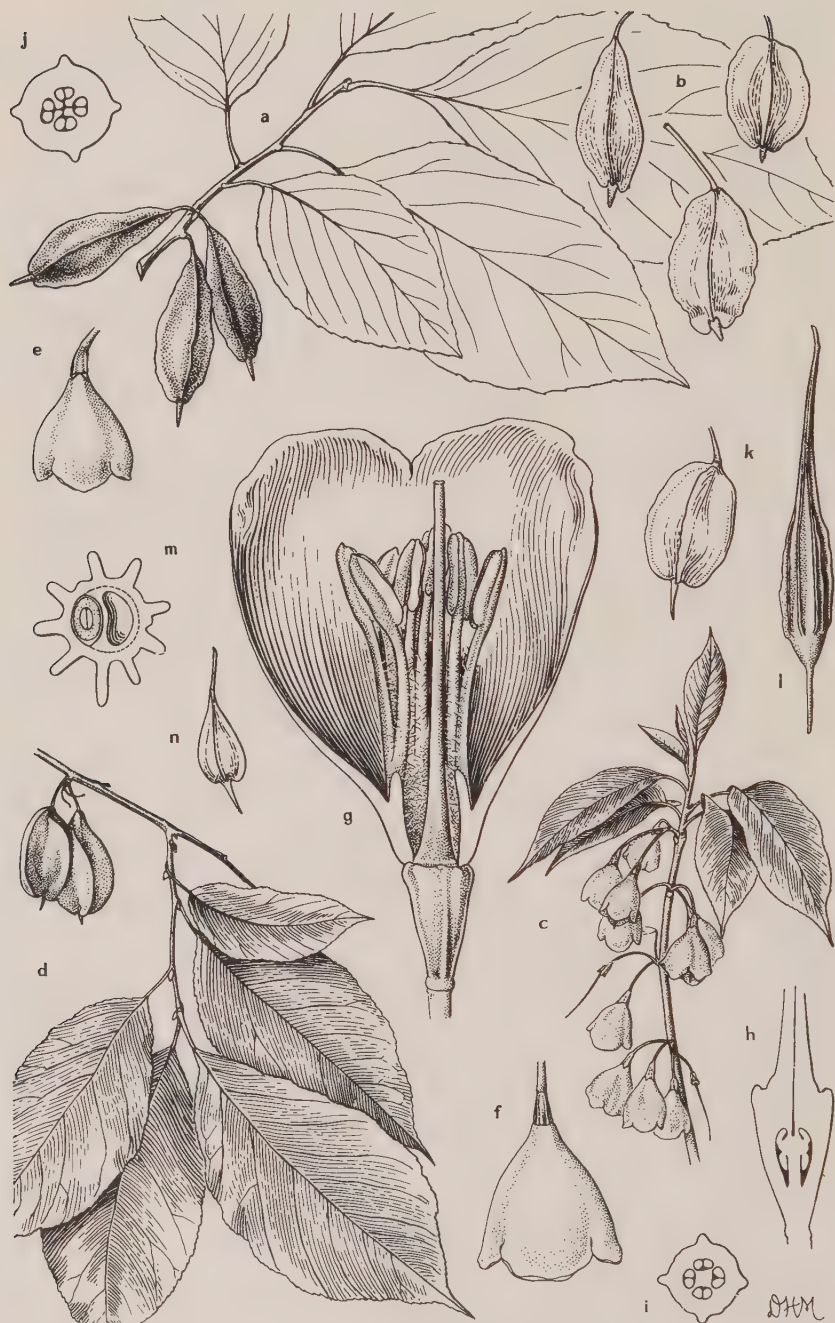


FIG. 4. *Halesia*. a, b, *H. diptera*: a, fruiting branchlet, $\times \frac{1}{2}$; b, fruit variants, $\times \frac{1}{2}$. c-e, *H. carolina* var. *carolina*: c, d, flowering and fruiting branchlets, $\times \frac{1}{2}$; e, flower, lateral view, $\times 1$. f-m, *H. carolina* var. *monticola*: f,

mouth of the Tennessee (Massac County, Illinois), suggesting migration along these routes by means of the floating, corky-winged fruit. An isolated series of stations occurs across central Arkansas into southeasternmost Oklahoma. Members of this complex have ovate to elliptic or oblong-obovate, acuminate, closely serrulate leaves; glabrous to tomentose pedicels and calyx; campanulate, shallowly lobed corollas 1–2.5 cm. long; 10–16 stamens; a 4-locular ovary; and 4-winged fruits 2–6 cm. long, with wings broad to narrow and rounded to long-tapering at the base. The extremes of the complex are distinctive, but the variation is puzzling and the taxa have not been carefully studied or clearly defined. One extreme, *H. monticola* (Rehd.) Sarg. (*H. carolina* var. *monticola* Rehd.), is a tree to 30 m. tall, of the higher mountains of North Carolina, Tennessee, and northern Georgia, with large corollas and large fruit with wings up to 15 mm. wide, truncate or rounded (and often widest) at the base. It appears to pass into *H. carolina* (*H. tetraptera* Ellis⁶), a shrub or tree to 10 m. tall, with

⁶ Although *Halesia tetraptera* Ellis long has been identified with *H. carolina* L., the name recently has been adopted for *H. parviflora* Michx. on the basis of the illustration in Ellis' paper (Trans. Roy. Soc. London 51: 931. pl. 22. 1761). From this illustration alone one may well conclude that the small flowers and tapering fruits illustrated are those of *H. parviflora* (described from St. Johns Co., Florida), but other evidence from the letters of Alexander Garden to John Ellis and from Ellis to Linnaeus (see J. E. Smith, A Selection of the Correspondence of Linnaeus, and Other Naturalists, from the Original Manuscripts 1: 82, 83, 88, 92, 93, 373–382. 1821) suggests that the usual disposition of the name is the more correct one. From this correspondence it is clear that the plant was collected "on the hills, 200 miles to the northwest of that city [Charleston, S. C.] at a place called Saluda [Saluda Co., S. C.]," where Alexander Garden went in the course of June and July, 1755. In the spring of 1756, Garden's brother-in-law, a Mr. Perroneau, took to Ellis "the branch with the fruit, and a sprig with the flowers," which were the basis of the illustration by Ehret in Ellis' paper, along with mature fruits which, although planted in June, 1756, did not germinate until May of the following year.

Thus, although Ellis' published account of *Halesia tetraptera* (quoting from Garden) noted only that the plant "grows commonly along the banks of Santee river," the more precise information places the type locality off the Coastal Plain and apparently within the range of *H. carolina*, rather than that of *H. parviflora*. The seedlings raised in England by Ellis were almost certainly *H. carolina*, for as recently as 1951, both Bean (Trees and Shrubs Hardy in the British Isles. ed. 7. 2: 80) and the Royal Horticultural Society Dictionary of Gardening fail to note *H. parviflora* in cultivation there, and the plant illustrated by Sims in 1806 (Bot. Mag. 23: pl. 910), with the comment that this was first raised in England by Ellis from seeds sent over by Dr. Alexander Garden in 1756, can be only *H. carolina*.

Finally, Ehret's illustration in Ellis' paper, having been prepared from dried specimens sent by Garden, must be considered in terms of the shrinkage of flowers and fruits in drying and of the habit of the corollas of opening when only half grown. Both of these phenomena may apply here. The fruiting branch illustrated (see also reproduction of Ehret's illustration in Rhodora 60: 86. pl. 1231. 1958) appears to represent *H. carolina* with the wings of the fruit somewhat shrunken in drying. The small flowering branch, on the other hand, bears flowers which appear to be not yet

flower, lateral view, $\times 1$; g, flower with two petals, eight stamens removed, $\times 3$; h, ovary, vertical section, $\times 4$; i, j, ovary, cross sections through lower and upper ovules, respectively, $\times 6$; k, fruit, $\times \frac{1}{2}$; l, endocarp from a very large fruit, $\times 1$; m, endocarp, cross section with seed, endosperm (stippled), embryo, and cavity, $\times 3$; h–j, m, semidiagrammatic. n, *H. parviflora*: fruit, $\times \frac{1}{2}$.

smaller corollas and smaller fruit with narrower wings often tapering into the pedicel. The other extreme, *H. parviflora* Michx., a shrub or tree to 10 m. tall, perhaps restricted to sandy woods and bluffs of the Coastal Plain from Georgia and Florida to Mississippi, but possibly entering the Piedmont, has, in its best development, small, rather flaring corollas about 1.2 cm. long, pubescent calyces, and fruits 2.5–3.5 cm. long with narrow wings 3–5 mm. wide tapering into the pedicels (thus giving the effect of a clavate fruit). Most distinctive in northeastern Florida, this plant appears to intergrade with *H. carolina*; plants from the central areas of South Carolina, Georgia, and Alabama need special study in this respect. Throughout this complex the shape and size of the stony endocarp seem to be roughly the same; the varying shape and width of the four wings produces the wide range of fruit-shapes. The length of the style seems also to be more or less constant: thus it is equalled or exceeded by the corollas of *H. carolina* (including *H. monticola*), but protrudes from the short, rather flaring corollas of *H. parviflora*.

The Chinese species, *H. Macgregorii* Chun, combines a deeply parted corolla (as in *H. diptera*), four-winged fruits (as in *H. carolina*), and eight stamens of two lengths (eight equal stamens in *H. diptera*). The ovary is said to be 3-locular. *Halesia* (with *Nyssa*, *Carya*, and a few others) is of interest in being a genus of the eastern American–eastern Asiatic distribution in which more representatives occur in America than in Asia. In most genera following this pattern the Asiatic contingent appears both to be more numerous and to include more primitive species than the American. *Halesia* is most closely related to *Pterostyrax* Sieb. & Zucc., (5 species, Japan, China, Burma), *Rehderodendron* H. H. Hu (9 species, China, Indochina), *Sinojackia* H. H. Hu (3 species, China), and *Melliodendron* Hand.-Mazz. (2 species, China).

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at full size and which are perhaps somewhat shrunken in drying. The details of the corolla illustrated are hardly compatible with fully developed corollas of either *H. carolina* or *H. parviflora*. Fruiting material shrunken in such a way may be matched by *Fox* 5265, Rutherford Co., N. C. (GH); *Duncan* 3349, Clarke Co., Ga. (A); and *Faxon*, Oct. 1896, cultivated, Jamaica Plain, Mass. (GH). An instructive series is formed by *E. J. Palmer* 20739, 20763, 26760 [20760?], April 11, 12, 1922, from near Page, LeFlore Co., Oklahoma (A): in these collections corollas of plants in various stages of development are approximately 2, 1.2–1.5, and 0.7 cm. long, respectively.

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SYMPLOCACEAE (SWEETLEAF FAMILY)

Trees or shrubs with alternate, simple, more or less coriaceous, exstipulate leaves, the nodes with one trace from one gap; complete, regular, sympetalous flowers; numerous[-4] stamens with ovate anthers; 2-5-locular inferior or half-inferior ovaries, typically with 2 pendulous, axile, 1-integumented ovules in each locule, and drupaceous or baccate fruits.

A small unigeneric family of approximately 300 species (placed in eight sections in four subgenera by Brand), of the warmer parts of America, Asia, and Australia (absent from Africa and Europe), the species very numerous in South America, about eight species ranging northward into Mexico, about 18 in the West Indies, and one in the United States, this primarily of our area, but extending into adjacent regions. Many of the species apparently are of local distribution, endemic to islands or mountains.

The Symplocaceae presumably are closely related to the Styracaceae, but differ in a number of characteristics: stamens usually in several series, often fasciculate (vs. stamens apparently in a single series in Styracaceae); ovate anthers (vs. oblong or linear anthers); inferior or half-inferior, completely loculed ovary (vs. superior to inferior, incompletely loculed ovary); baccate or drupaceous fruit (vs. dry, capsular to indehiscent fruit); simple hairs (vs. stellate or peltate hairs); usually rubiaceous stomata (vs. ranunculaceous stomata); solitary vessels with elongated pits between vessels and rays in the secondary wood (vs. solitary or clustered vessels with small, round pits between vessels and rays); and the occurrence of spiral thickenings in the vessels, commonly, and in the fibers, occasionally (vs. the lack of such thickenings).

The family is of limited economic importance. A few species are sometimes used for their wood, the leaves and bark of several (including *S. tinctoria*) yield a yellow dye, the roots of some are used in the preparation of tonics, and the leaves of several species are used as a substitute for *maté* (primarily from *Ilex* species). *Symplocos paniculata* (Thunb.) Miq.

(subg. *HOPEA*, sect. *BOBUA*), with terminal clusters of white flowers and methyl-blue fruits, and a few other Asiatic species are sometimes grown as ornamental shrubs.

The biological features of the group seem to have been studied hardly at all.

1. *Symplocos* Jacquin, Enum. Syst. Pl. Carib. 5. 1760; Select. Stirp. Am. Hist. 166. *pl.* 175, *fig.* 68. 1763.

Deciduous or tardily deciduous shrubs or trees with more or less coriaceous, sweet-tasting leaves. Flowers in congested or open, racemose or paniculate inflorescences, in ours about 6–14 in short, sessile, close clusters or racemes axillary to leaves or their scars, yellow, fragrant. Calyx adherent to the lower portion of the ovary, persistent, the 5 lobes valvate or imbricate. Corolla sympetalous, 3–11-lobed, deeply 5-lobed in ours, the tube short. Stamens [4–]many, conspicuous, exserted, in several unequal series, epipetalous at the base of the corolla, [free or monadelphous, the filaments connate in a tube, or] in ours pentadelphous, in 5 groups alternate with the corolla-lobes, the innate anthers short, orange, the filaments slender, white, distinct except at the base. Pollen usually 3-colpate. Gynoecium syncarpous; stigma terminal, slightly dilated or capitate, minutely lobed; style linear, the ovary inferior or half-inferior, in ours surrounded at the top by an orange-colored disc of nectariferous spongy tissue, 3 [2–5]-locular; placentation axile, the anatropous (?) 1-integumented ovules pendulous, typically 2 in each locule. Fruit drupaceous [or baccate], in ours cylindric-ellipsoid, about 1 cm. long; usually only a single seed developing; embryo straight [or curved], with short cotyledons, and with copious endosperm. (*Hopea* L. f., 1767, not Roxb., 1814.) TYPE SPECIES: *S. martinicensis* Jacq. (The name from Greek, *symplokos*, connected, twisted, entwined, apparently referring to the union of the stamens with each other and with the petals in *S. martinicensis*.)

Symplocos tinctoria (L.) L'Her., sweetleaf, horse-sugar, wild laurel, or yellow-wood, the only species indigenous to the United States, occurs from Sussex County, Delaware, southward to northern Florida and westward to eastern Texas and southeastern Oklahoma. Varietas *tinctoria*, with glabrous fruits, glabrous or glabrate current stems and tardily deciduous leaves, is widespread on the Coastal Plain, where it is largely restricted to hammocks, the margins of swamps and to sandy soils in association with *Pinus*, *Nyssa*, *Persea*, *Magnolia*, etc. Varietas *Ashei* Harbison, with pubescent fruits, persistently hairy stems, and promptly deciduous leaves, is distributed over a limited region of the southern Appalachians in western North and South Carolina, northern Georgia, and southeasternmost Tennessee (a single station in Polk County), between 1800 and 4500 feet in altitude, on dry ridges of chiefly acid, red-clay soils, where it is associated with *Pinus rigida* Mill., *Quercus coccinea* Muenchh., *Q. prinus* L., and (formerly) *Castanea dentata* (Marsh.) Borkh. It appears largely to be lacking between mountains and Coastal Plain, although scattered sta-

tions may be expected in the Piedmont and are known from at least Aiken County, South Carolina, and Wake County, North Carolina. The geographical isolation of these varieties can be determined only after additional stations are sought, particularly in the Piedmont and in northern Alabama (where the species has been reported as far north as Marion, Cullman, and Morgan counties). Varietas *pygmaea* Fern., based upon dwarf, sterile specimens with small leaves, from white sands of dry pine barrens in Isle of Wight County, southeastern Virginia, is doubtfully distinct. The typical variety occurs in abundance in this general area of the state.

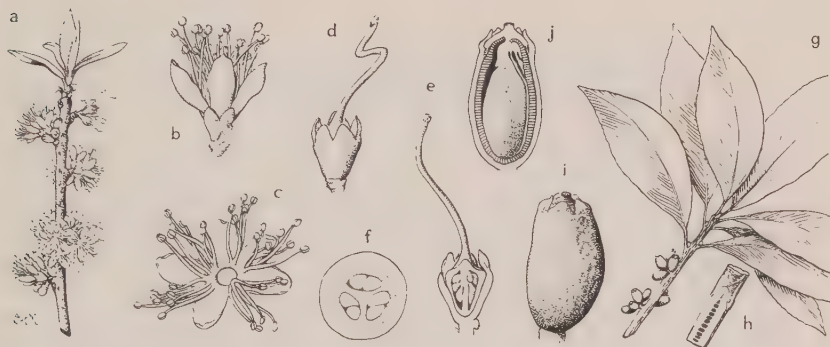


FIG. 5. *Symplocos*. a-j, *S. tinctoria* var. *tinctoria*: a, flowering twig, $\times \frac{1}{2}$; b, flower, $\times 2$; c, detached corolla with stamens, $\times 2$; d, flower with corolla removed, $\times 3$; e, same, the ovary in vertical section (semidiagrammatic), $\times 3$; f, cross section of ovary at anthesis — stippled area becomes sclerified in fruit (semidiagrammatic), $\times 6$; g, fruiting twig, $\times \frac{1}{4}$; h, portion of twig in oblique section to show diaphragmed pith, $\times \frac{1}{2}$; i, mature fruit, $\times 2$; j, mature fruit, vertical section, the fertile locule with seed to left and center, abortive locules to right, $\times 2$.

Characteristically a shrub, *Symplocos tinctoria* occasionally attains arborescent proportions (nearly 30 cm. in diameter and 12 m. tall) in the fertile river bottoms of Mississippi which usually are inundated for several weeks of the year.

Brand placed *Symplocos tinctoria* near *S. japonica* A. DC. and *S. setchuensis* Brand as the only American species of subg. HOPEA (L. f.) C. B. Clarke, sect. PALAEOSYMPLOCOS Brand, a group distinguished on the basis of the 3-locular ovary and clearly pentadelphous stamens with filiform filaments. However, because the summit of the ovary is glabrous and the united portion of the stamen-filaments is flattened (instead of round in section), Handel-Mazzetti and Peter-Stilbal excluded *S. tinctoria* from the subgenus (which was then renamed as subg. EOSYMPLOCOS), suggesting that its relationships should be sought among the New World species. Inconsistently, sections LODHRA and BOBUA (also of subg. HOPEA) were defined by the latter authors to include species with the apex of the ovary either glabrous or pubescent! It may be significant that at least some speci-

mens of *S. tinctoria* var. *Ashei* have a few hairs on the summit of the ovary at anthesis.

The subdivisions of *Symplocos* have been treated by some authors as separate genera, although most have maintained the group as a single genus with well-marked subgenera or sections. Erdtman, noting a variety of pollen types in *Symplocos*, suggests that pollen morphology "may be instrumental in subdividing the genus (or — if considered appropriate — in referring the different species to a number of genera now usually regarded as sections etc. under *Symplocos*)."

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THE ARNOLD ARBORETUM

AND

VANDERBILT UNIVERSITY

A TAXONOMIC REVISION OF *PODOCARPUS*, XII. SECTION *MICROCARPUS*

NETTA E. GRAY

PODOCARPUS USTUS (Vieillard) Brongniart and Gris, the only species in section *Microcarpus*, is a very curious, small, twiggy shrub found in several places in the mountain forests of New Caledonia. Vieillard and Deplanche, the first collectors, said that the local residents regarded this plant as sacred and attributed marvelous properties to it. The scale-like leaves, similar to some found in section *Dacrycarpus*, are arranged spirally, covering the surface of the twig and adnate to the stem, often with only a millimeter of free leaf blade. A figure showing a vegetative branch and seeds is shown by Pilger (4, 5) in both of his treatments of the genus.

The species has been collected several times since it was described by Vieillard in 1862, but only the most recent collection, that of De Laubenfels (2) in 1957, has shown it growing parasitically on *Dacrydium taxoides* Brongn. & Gris. The color of the plant is variously described as reddish, copperish, bronze, or purple. As Luc Chevalier (1) describes it most recently, "ses rameaux dressés ressemblent à une branch de corail rouge et les cônes femelles au bout des rameaux sont d'un bleu roi légèrement argenté." Indeed, when I soaked some twigs in water in preparation for examination of the leaves, the water turned very reddish purple, the effect of known anthocyanins. In view of the possible absence of chlorophyll, a test was made by analyzing an alcoholic solution from the leaves in a Beckman photospectrometer. The absorption curve showed the drop at 650 millimicrons indicative of the presence of chlorophyll *a*.* These results indicate that the specimen examined most probably was not completely parasitic. It is interesting to note in this connection that the history of the collections shows, in almost every case, that *Dacrydium taxoides*, the host of this specimen, was collected at the same time as *Podocarpus ustus*. Since the knowledge of its semi-parasitic nature became available no further collections have been obtained, but one may reasonably suspect that the plant may prove to be a root-parasite on *Dacrydium* or other gymnosperms.

Podocarpus ustus (Vieillard) Brongniart & Gris, Bull. Soc. Bot. France 13: 426. 1866; Parlato in DC. Prodr. 16: 521. 1868; Gordon. Pinetum ed. 2. 358. 1875; Warburg, Monsunia 1: 193. 1900; Pilger. Pflanzenr. IV. 5(Heft 18): 58. 1903, Nat. Pflanzenfam. ed. 2. 13:

* The author wishes to express her great appreciation to Dr. Herbert Irvin, of the Crime Laboratory, Department of Public Safety of the State of Georgia, for his chlorophyll determination on *De Laubenfels P165*.

245. 1926; Guillaumin, Ann. Mus. Col. Marseille II. 9: 269. 1911, Bull. Mus. Hist. Nat. Paris 18: 100. 1912, Fl. N. Caledonia 11. 1948; Compton, Jour. Linn. Soc. Bot. 45: 425. 1922; White, Wilson & Guillaumin, Jour. Arnold Arb. 7: 77. 1926; Florin, Svenska Vet.-Akad. Handl. III. 10: 270. 1931; Dallimore & Jackson, Handb. Conif. 58. 1923, 1931, 84. 1948.

Dacrydium ustum Vieillard, Ann. Sci. Nat. Bot. IV. 16: 56. 1862; Carrière, Conif. 697. 1867.

A shrub, usually less than 1 meter tall, with dense, short, erect spreading branches, with the twigs entirely clothed by the copperish to purple or red, spirally placed, persistent adpressed scale leaves (FIG. 1), and with the terminal meristems protected by the youngest leaves. Leaves triangular, carinate, with broadly decurrent bases, 1–2 mm. long, 1–1.5 mm. broad; midribs not evident. Leaves differentially amphistomatic, having few stomata on the adaxial surface. Leaves without hypodermis or palisade parenchyma. Male strobili terminal and solitary on axillary leaf-covered peduncles up to 6 mm. long, the strobili short-cylindrical, 5 mm. long. Microsporophylls imbricate, sessile, 1.5–2 mm. long, 2-locular, longitudinally dehiscing; apiculi flat, thin, and broadly triangular. Female strobili terminal; peduncles 2–5 mm. long, clothed in decussate scale leaves, the uppermost not decurrent, succeeded on the strobilus by about 5 spirally placed longer bracts increasing to 2.5 mm. with longer internodes and blades free from the axis; fertile bracts usually only one, sometimes two, terminal, mostly free from the ovules; no fleshy receptacle. Seed globose, purplish, to 2.5 mm., not crested but often drying so there is an apparent acute apex.

DISTRIBUTION: In forests on mountain slopes, up to 1000 m. altitude, in New Caledonia.

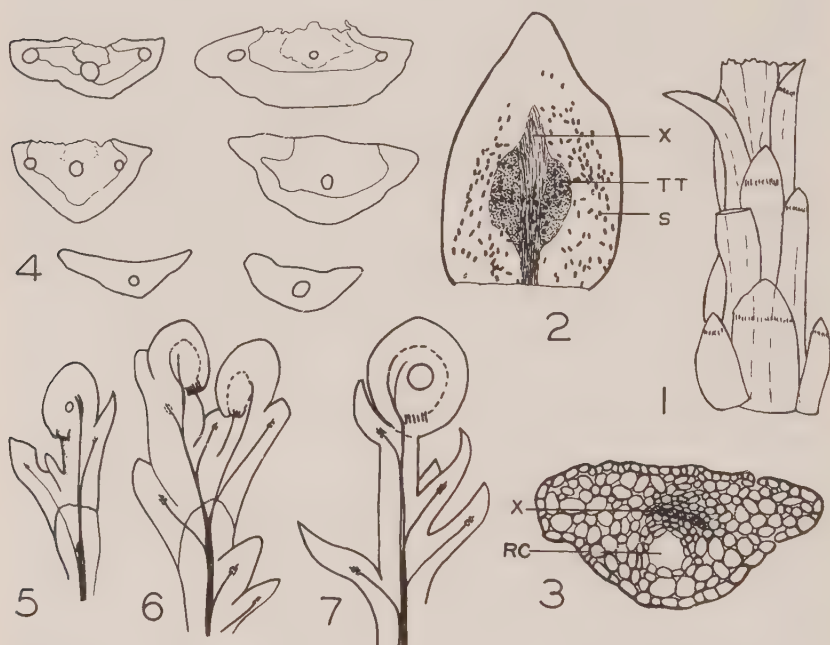
New Caledonia: Ignambi, *Compton 1545* (κ *); Pic de Pouébo, *Vieillard 1269* (P), *Deplanche 170* (P); Mt. Penari, *Balansa 3484, 3485* (P); Koe, *Balansa 184* (†P); Mt. Koghi, *Brousmiche 456, 601* (P); Dumbea, *Vieillard 1262* (P); slopes above Rivière Bleue, *De Laubenfels P165* (†GA); Forêts bas du Pic, des Sources, *LeRat 903* (†P); Montagnes de Poila, *Vieillard 1267* (†P-Type; †A, κ); Baie de Prony, *Jeanneney* (P). No specific locality: *Balansa* (BM, κ, †NY); *Pancher*, 1879 (†BR, κ); *Hennecart* (BR, †P, †UCLA).

In contrast to the leaves of most other podocarps, which are noted for the variety of cell types in their tissues, there is little differentiation in the mesophyll of the leaves of *Podocarpus ustus*. The walls of the epidermal cells are mostly simple, and the often abundant stomata are mostly on the

* The following symbols indicate the location of the specimens cited: Arnold Arboretum (A); British Museum (Natural History) (BM); Brussels Botanical Garden (BR); University of California at Los Angeles (UCLA); Herbarium of the University of Georgia (GA); Royal Botanic Gardens, Kew (κ); New York Botanical Garden (NY); Muséum National d'Histoire Naturelle, Paris (P).

† This symbol preceding the abbreviation of an herbarium signifies that the details of the leaves of this specimen have been examined in transverse section.

abaxial surface. The stomata are not arranged in rows, nor are they always oriented longitudinally (FIG. 2), merely being scattered over the surface. Only the smallest amount of vascular tissue connects with that of the stem and there is little vascular tissue in the free part of the blade of the leaf. Just before the bundle disappears the xylem tracheids shorten exceedingly and the vein broadens, with definite short wings of transfusion tissue on each side (FIG. 2), altogether giving a fan-like appearance to the termination of the bundle. The resin canal may continue beyond the end of the bundle but it rarely reaches the tip of the leaf; three resin canals may be present (FIG. 4). The blade of the leaf is swollen or fleshy and packed with roundish cells without conspicuous air spaces between them (FIG. 3). There is no palisade parenchyma and only rarely are a few isolated sclereids of the transfusion type seen.



FIGURES 1-7. *Podocarpus ustus*. 1, Part of stem, showing scale-leaves (*Vieillard* 1267), $\times 5$. 2, Cleared leaf, showing vascular tissue and stomata in abaxial epidermis (*De Laubenfels* P165), $\times 16$; S = stoma, X = xylem, TT = transfusion tissue. 3, Camera lucida outline of transverse section of leaf (from *De Laubenfels* P165), showing homogeneous mesophyll and resin canal (RC), $\times 35$. 4, Outlines of transverse sections of leaves to show shape and one to three resin canals (*Balansa* 184, 3485), $\times 15$. 5-7, Cleared ovulate strobili, all from *De Laubenfels* P165, $\times 7$: 5, strobilus with very young ovule; 6, strobilus with two young ovules; 7, strobilus with older ovule.

The solitary ovules are terminal on the twigs (FIGS. 5-7). As in other podocarps, a single vascular bundle enters the ovuliferous scale but almost

immediately divides, both branches arching over the back to the top of the ovule. One of the specimens of *De Laubenfels P165* has pairs of ovules (FIG. 6) and close examination shows them to be separate on the uppermost bracts.

The lack of hypoderm in the leaves and the lack of a fleshy receptacle below the ovule definitely separate this species (and thus section *Microcarpus*) from section *Dacrycarpus*. If the scale leaves of *Podocarpus ustus* be considered merely evidence of modification toward the parasitic habit, then the species seems to be more closely related to section *Stachycarpus* where the other characters are typical. This position in the genus would be in better accord with the recent genetic studies in *Podocarpus* by Hair and Beuzenberg (3) who found that *P. ustus* has a diploid chromosome number of 36. They found chromosome numbers of 36 and 38 in section *Stachycarpus* and a diploid number in section *Dacrycarpus* of only 20.

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AGNES SCOTT COLLEGE
DECATUR, GEORGIA

STUDIES IN THE GENUS COCCOLOBA, VIII.
NOMENCLATURAL CHANGES

RICHARD A. HOWARD

SINCE THE PUBLICATION of the preceding papers in this series several matters involving nomenclatural changes have come to my attention. These changes concern *Coccoloba novogranatensis*, a species of the Lesser Antilles, Trinidad and northern South America, and *C. nitida* and *C. guianensis*, species of South America. In making the necessary corrections, two Vellozo names must be considered and the species concepts of the previous monographers Meisner and Lindau altered for additional taxa.

Coccoloba novogranatensis

Dr. Armando Dugand has called my attention to a paper of his which was published in *Caldasia* in 1947. I was not aware of this paper in which *Coccoloba coronata* Jacquin is properly identified and in which *Coccoloba novogranatensis* Lindau is placed in the synonymy of the Jacquin species. I do not agree completely with Dugand's treatment, since the proper citation for this species, with additional synonymy, appears to be the following:

Coccoloba coronata Jacquin, Enum. Pl. Carib. 19. 1760, Select. Stirp. Amer. Hist. 114. *t.* 77. 1763; Dugand, *Caldasia* 4: 427. 1947, not Lindau, Symb. Ant. 1: 228, 229. 1899.

Coccoloba virens Lindl. Bot. Reg. 21: *t.* 1816. 1835.

Coccoloba novogranatensis Lindau, Bot. Jahrb. 13: 192. 1890; Howard, Jour. Arnold Arb. 40: 85-87, 208-9. 1959.

Coccoloba dioica Karsten ex Lindau, Bot. Jahrb. 13: 170. 1890.

Coccoloba caribaea Urban, Symb. Ant. 5: 337. 1907.

Coccoloba waittii Johnston, Sargentia 8: 122. 1949.

The type location for Jacquin's species was cited as Cartagena. Dugand, who is familiar with this area and its vegetation, could not find constant or significant characters to separate *Coccoloba coronata* Jacq. from *C. novogranatensis* Lindau and concluded that they were identical. I can agree with him on this. However, Dugand accepts the synonymy given by Lindau (i.e., that *C. punctata* L. and *C. coronata* Jacq. are the same), but I can not agree with this. Lindau's treatments of *C. excoriata*, *C. punctata*, and *C. venosa* in his monograph of the genus (Bot. Jahrb. 13: 106-229. 1890) and in his later treatment of the West Indian species for Symbolllae Antillanae (1: 229. 1890) are confused. This has been discussed previously by Fawcett and Rendle (Jour. Bot. 51: 123. 1913) and by me (Jour. Arnold Arb. 30: 398. 1949). *Coccoloba punctata* L. (Sp. Pl. ed. 2.

523. 1762) is not the same as *C. coronata* Jacq., but is a synonym of *C. venosa* L. The name *Coccoloba punctata* L. does not belong among the synonyms given by Dugand.

Coccoloba virens Lindl. was illustrated in the *Botanical Register* on the basis of a specimen which flowered in a British greenhouse in 1833. The place of origin for this plant is uncertain. Lindau first referred this species to the synonymy of his "*Coccoloba punctata*" (Bot. Jahrb. 13: 160. 1890) and later to his "*Coccoloba coronata*" (Symb. Ant. 1: 228. 1899). *Coccoloba virens* Lindl. can not be the true *Coccoloba venosa* L. to which Lindau's "*C. coronata*" and "*C. punctata*" belong, but it is the present species *Coccoloba coronata* Jacq.

Lindau described *Coccoloba dioica*, using a manuscript name appearing on an embossed label of a Karsten collection in the Leningrad herbarium. In spite of the specific epithet and the notes on the collection, Lindau failed to note the unisexual nature of the flowers in the published description. The Karsten specimen represents a pistillate plant, as the flowers have rudimentary stamens with abortive anthers and no pollen. In a key to the species in his monograph, Lindau distinguished between his *C. novogranatensis* and *C. dioica* by the fact that the former has a pubescent, and the latter a glabrous, lower leaf surface. The Karsten type, which I have been privileged to study, has leaves with pubescence along the midrib and on the primary veins. There is no doubt that the type specimens are comparable and that *C. dioica* can be assigned to the synonymy of *C. coronata*.

Coccoloba caribaea Urban and *C. waittii* Johnston have been placed in synonymy and discussed in earlier papers (Jour. Arnold Arb. 40: 86, 209. 1959).

Coccoloba nitida

A second correction involves the use of the names *Coccoloba nitida*, *C. marginata*, and *C. guianensis* by Meisner, Lindau and Howard, the three monographers of the genus. In an earlier study (Jour. Arnold Arb. 40: 83-85. 1959) I accepted the interpretation of *C. nitida* as published by Lindau and as indicated by his annotations on specimens. I had not seen the Humboldt type specimen of *C. nitida*, and, in fact, made an additional error in considering still another worker's photograph and annotation of a Martius specimen as the type of the species. Although Lindau cited a Humboldt collection from Colombia in his treatment of the species, he did not state specifically in which herbarium this specimen was located. The collections of *Coccoloba* of the Berlin herbarium, including the Willdenow herbarium, which I have now seen, do not contain such material. Recently, through the kindness of the Director of the Muséum National d'Histoire Naturelle, Paris, I have examined a sheet labelled primarily "*Coccoloba laurifolia* Knth.," with a smaller annotation of "*C. nitida*." This specimen was collected at S. Bartholome on the Río Magdalena in May, 1805, and is numbered 1627. This must be the type of *Coccoloba nitida* H. B. K., for it agrees with the original description of the species.

However, it does not agree with Lindau's description of *Coccoloba nitida*, nor with the specimen he has so annotated. Lindau apparently did not see the type of *C. nitida*. Even though he cited the collection, the only available specimen of it does not bear his annotation. The Paris specimen mentioned is a poor one, consisting of a single short stem with a terminal inflorescence and one and one-half detached leaves. The leaves are insect infested and are abnormal at the tips. The specimen, however, has distinctive characteristics in the spathe-like basal ocrea of the inflorescence, the distinctive ridging of the pubescent rachis, and the closely packed fascicles of pedicels and buds.

It is clear now that *Coccoloba nitida* is properly typified by the Humboldt collection. As such, it is a distinctive species of Colombia, and the synonymy and citation of specimens given in my earlier papers, as well as those of Meisner in the Flora Brasiliensis and of Lindau in his monograph, are incorrect.

To the synonymy of *Coccoloba nitida* H. B. K. must be added *C. microneura* Meisner. Through the courtesy of the Director of the Royal Botanic Gardens, Kew, I have been able to study the Purdie specimen which is the type of *C. microneura*. In the original description, Meisner attributes the specimen he saw to the Arnott herbarium, but no material of this species could be found in the Prodrum or Delessert herbaria in Geneva. Lindau, however, saw the specimen at Kew. The Purdie specimen, without number, was collected in Santa Marta, Colombia, and is a full and ample specimen in flower. The species is not known in fruit. While the leaves are somewhat smaller than the type of *Coccoloba nitida* in all reliable characters, it is evident that *C. microneura* and *C. nitida* are conspecific. The correct nomenclature and the specimens examined follow.

***Coccoloba nitida* H. B. K. Nov. Gen. Sp. 2: 176. 1818.**

Coccoloba microneura Meisner, DC. Prodr. 14: 163. 1856.

Colombia. San Bartholome on Río Magdalena, *Humboldt* 1627 (p-lectotype); Santa Marta, *Purdie s.n.* (x-type of *C. microneura*); Dept. El Magdalena, Chimi-chaguá, *Haught* 2228 (F, M, NY).

Recently I described *Coccoloba darienensis* (Jour. Arnold Arb. 40: 159. 1959) based on *Allen* 934, a fruiting specimen from Darien, Panamá. There are minor differences in the number of veins and the general aspect of the leaf, but the close relationship of *C. darienensis* to *C. nitida* is obvious. It is possible that additional collections of either species may prove them to be the same and that the range of *C. nitida* should be extended to Panamá.

There is still the question of what is the remainder of the *Coccoloba nitida* concept of Meisner, Lindau and Howard when the Humboldt type is removed and the name applied to an endemic species of Colombia. Of the suggested synonyms of these authors, a Vellozo name is the oldest and most troublesome.

Polygonum arborescens

Polygonum arborescens Vellozo was described in *Florae Fluminensis* 162. 1825, and illustrated in the *Icones* (4: t. 43. 1827). The location given as "Habitat silvis maritimis ad ripas fluvii vulgo dicti Taguahy, atque etiam fruticetis Parochiae Campo-grande" can not be located exactly on modern maps, but is presumed to be near the town of Santa Cruz, in the Federal District, or in the western half of the State of Rio, Brazil.

Meisner (*Fl. Bras.* 5(1): 38. 1855) refers the species with a question to the synonymy of *Coccoloba nitida* H. B. K. Meisner's concept of *C. nitida* was the first broad one which ignored the Humboldt type and was one which I now consider to be incorrect. Lindau also maintained this erroneous concept and also considered *Polygonum arborescens* Vellozo as a possible synonym of *C. nitida*.

Vellozo's description is brief, but the illustration shows several significant characteristics of aid in identifying this plant. It is obviously a liana, with well-developed short-shoots and persisting, nearly foliaceous ocreae which split into lanceolate "stipules." The flowers are on short pedicels in the inflorescence but the pedicels elongate in fruiting condition. On these characteristics the plant is surely the same as *Coccoloba crescentiifolia* Chamisso, and a new combination, *Coccoloba arborescens*, must be made. There is a second Vellozo species and illustration which has been referred to *C. crescentiifolia* which must be considered.

Polygonum frutescens

Polygonum frutescens Vellozo (*Flor. Flum.* 162. 1825, *Icones* 4: t. 44. 1827) has had an unstable history. Vellozo's description of this is short ("P. spica simplici, terminali"), but he reports that it occurs in locations similar to his *Polygonum arborescens*. I can not refer the illustration of *P. frutescens* with real conviction to any currently recognized species. I believe that it may represent a terminal scrambling shoot of Vellozo's *Polygonum arborescens*. However, without knowledge of the ocreae (which can be interpreted in the drawing as deciduous or very short), the point of attachment of the petioles, and the curvature and pubescence of the blade, this can be only an attempt at an intelligent guess.

Casaretto was the first to consider *Polygonum frutescens* Vellozo. He cited this name in synonymy when he described *Coccoloba vellosiana* (*Novarum Stirpium Brasiliensium* Decades 70. 1844.) Casaretto's species, while honoring Vellozo, must be considered to be based on an unnumbered Riedel collection from the vicinity of Rio de Janeiro. Throughout the description Casaretto credits Riedel for the data supplied. The unnumbered collection to which Casaretto refers must be *Riedel 674*, for the descriptive data on the label "In sylvaticis maritimis inque collib. ciccis R. Janeiro Jul. 1832" compare favorably, although not verbatim, with those given by Casaretto, "Habitat in arenosis maritimis et collibus siccis circa Rio de Janeiro (Riedel)."

In 1855, Meisner (Fl. Bras. 5(1): 36.) reduced *Polygonum frutescens* Vellozo to the synonymy of his new species *Coccoloba gardneri*. He also cited in synonymy *C. vellosiana* Casaretto, although with a question mark. Meisner cited only *Gardner 600* from the Serra dos Orgãos, Prov. Rio de Janeiro. I have examined this collection, but fail to find any similarity with the illustration of *Polygonum frutescens* Vellozo, and therefore believe that *Coccoloba gardneri* should be reestablished as a valid species for the consideration of future collectors in the Rio area. The type of this species is *Gardner 600* and the synonymy given by Meisner should be excluded.

In 1833, Chamisso described *Coccoloba crescentiifolia* (Linnaea 8: 134–136.), basing the species on an unnumbered Sellow collection from “Brasilia.” Four specimens bearing labels inscribed “*Coccoloba crescentiaefolia* N” are in the herbaria at Berlin, Leningrad and Munich. The specimens in the Munich herbarium bear a further note which indicates that the collection was made near “Praya grande, prov. Rio de Janeiro.”

In his monograph (Bot. Jahrb. 13: 173. 1890) Lindau accepted *C. crescentiifolia* Cham., but placed in its synonymy *C. vellosiana* Casar. and *C. gardneri* Meisner, as well as *C. fasciculata* Weddell. He also listed in the synonymy, with a question mark, *Polygonum frutescens* Vellozo, as Meisner had done earlier. Lindau also included in his citation of specimens the collection *Gardner 600*. Thus, none of the monographers has been certain of the interpretation of *Polygonum frutescens* Vellozo, but all agree on the possibility of its being the same as *Coccoloba crescentiifolia*. If further collections or study prove this to be true, the acceptable name will be *Coccoloba arborescens* (Vellozo) Howard, since no combination of the Vellozo names has been made previously. If further study should show *Polygonum frutescens* to be distinct from *Coccoloba arborescens* (*C. crescentiifolia* Cham.), then the Vellozo name, being the oldest in use in the Rio area, must be adopted over some other currently accepted name. The correct nomenclature for the concept involving *Coccoloba crescentiifolia* Chamisso is the following:

***Coccoloba arborescens* (Vellozo) Howard, comb. nov.**

Polygonum arborescens Vellozo, Flor. Flum. 162. 1825, Icones 4: t. 43. 1827.
Coccoloba crescentiifolia Chamisso, Linnaea 8: 134. 1833, “*crescentiaefolia*.”
Coccoloba vellosiana Casaretto, Nov. Stirp. Bras. Decad. 70. 1844.
Coccoloba fasciculata Weddell, Ann. Sci. Nat. III. 13: 258. 1849.
Coccoloba crescentiifolia var. *obtusata* Meisner, Fl. Bras. 5(1): 26. 1855.

Coccoloba fasciculata Weddell, based on *Blanchet 769*, was distinguished from *C. crescentiifolia* on the basis of flat leaves which were less rigid and had shorter petioles. The specimens which I have seen of this collection are of short lateral branches, and there is no doubt that the collection should be identified as *C. arborescens*.

Meisner's taxon *Coccoloba crescentiifolia* var. *obtusata* was based on *Claussen 2013*. The characteristics Meisner indicated as distinguishing this variety are not consistent in the several examples of the collection

which I have seen. As Lindau has already indicated, the variety is not worthy of recognition.

Returning now to Lindau's concept of *Coccoloba nitida*, two synonyms are easily removed from further consideration. *Coccoloba pendula* Salzmann first was published in synonymy by Meisner (Fl. Bras. 5(1): 38. 1855), and *C. recurva* Newman was placed in synonymy by Lindau (Bot. Jahrb. 13: 180. 1890). The specimens labelled "C. pendula Salzm." at Leningrad and Paris are to be referred to *C. marginata* Benth., a name to be considered shortly. I have been unable to find material labeled "C. recurva Newman" at Geneva and am unable to associate this name. The reference "Coccoloba foliis cordato-oblongis Plum. Pl. am. 137 tab. 146 f. 1" referred with a question to *Coccoloba nitida* by Lindau. Urban (Repert. Spec. Nov. Beih. 5: 69-70. 1920) has referred the Plumier illustration and reference to the species now known as *C. venosa* L. I am not convinced that either author is correct. The origin of the material which Burmann illustrated is not certain. As Urban suggested that it may have come from Trinidad, I believe its correct identity is *C. marginata*.

The specimens Lindau cited in his monograph as *Coccoloba nitida* are to be distributed among *C. arborescens*, *C. marginata* and *C. nitida*. Although I have not seen the collections Lindau cited from Dutch and British Guiana, I suspect that these will prove to be *C. marginata*. Friedrichsthal 398, reported from Guatemala, was cited by Meisner in the original description of *C. martii*. The specimen was attributed to the Vienna herbarium and was reported to have come from "S. Thomas, Guatemala." Lindau placed *C. martii* in the synonymy of his *C. nitida* and cited the Friedrichsthal collection. All of the material of *Coccoloba* in the Vienna herbarium was lost during World War II, so the identity of this collection may never be established. I have not seen specimens of *C. arborescens*, *C. marginata*, or *C. nitida* in the collections from Guatemala which I have already studied.

Coccoloba guianensis

In a review of *Coccoloba* in the Lesser Antilles, Trinidad and Tobago, I accepted the name *C. nitida* with six taxa as synonyms. The correct name for this species should be *C. marginata* Benth., with the following synonymy:

Coccoloba marginata Benth., London Jour. Bot. Hooker 4: 626. 1845.

Coccoloba guianensis Meisner, Linnaea 21: 264. 1848.

Coccoloba martii Meisner, Fl. Bras. 5(1): 37. 1855.

Coccoloba martii var. *major* Meisner, Fl. Bras. 5(1): 38. 1855.

Coccoloba martii var. *minor* Meisner, loc. cit.

Coccoloba nitida var. *rotundata* Meisner, loc. cit.

Coccoloba nitida var. *cordata* Meisner, loc. cit.

Coccoloba trinitatis Lindau, Bot. Jahrb. 13: 182. 1890.

Coccoloba douradensis Glaziou, Bull. Soc. Bot. France. IV. 11(Mem. 3f): 571. 1911 (provisional name with mixed type).

Lindau recognized *Coccoloba guianensis*, *C. marginata*, and *C. trinitatis* as distinct species. He considered *C. martii* a synonym of his *C. nitida*. I have indicated in an earlier paper (Jour. Arnold Arb. 40: 84. 1959) the variations in habit and leaf shape found on one plant of *C. marginata* in Trinidad, and I remain convinced that *C. marginata*, *C. guianensis*, and *C. trinitatis* are one and the same species. *Coccoloba guianensis* is the well known and widely used name for this species. *Coccoloba marginata*, the oldest name for the complex, was considered distinct only on the basis of the slightly recurved leaf margin. The type of *C. marginata* is Schomburgk's second collection numbered 118 (216) from British Guiana. The holotype is in the herbarium at Kew and an isotype is in Paris. All of the specimens which I cited as *C. nitida* in an earlier paper must be renamed *C. marginata* Benth.

Coccoloba martii Meisner is typified by a Martius collection from the vicinity of Salgao, on the river San Francisco, in Minas Geraës, Brazil. The specimen illustrates the nonscrambling aspect of the species.

Coccoloba douradensis Glaziov was used in a list of Glaziov collections with a question as to its status as a new species. Because only four words were used to describe the plant, the name should be considered a nomen nudum. The collection cited, *Glaziov 21978*, may prove to be a mixture. As has happened with other numbers of the Glaziov collection, the specimens and associated labels or numbers were mixed in the field or in distribution to herbaria. Sheets labeled *Coccoloba douradensis*, *Glaziov 21978*, may be referred to *Coccoloba densifrons* or to *C. marginata*.

THE GENERA OF THE ARALES IN THE SOUTHEASTERN
UNITED STATES¹

KENNETH A. WILSON

THE ARALES (Spathiflorae), in the view of most authors, include only the families Araceae and Lemnaceae, the latter representing highly reduced plants of aroid ancestry. A much broader interpretation of the order is the one of Wettstein, who included in his "Spadiciflorae" not only the Araceae and Lemnaceae, but also the Palmae and Cyclanthaceae. Other authors (e.g., K. Fritsch, *Ber. Deutsch. Bot. Ges.* 50a: 162-184. 1932) have interpreted this group as including also the families Pandanaceae, Sparganiaceae, and Typhaceae. Such an interpretation of the order is subject to considerable disagreement, and these families may indeed not be very closely related to each other. The Arales are here interpreted in the Englerian sense to include only the families Araceae and Lemnaceae, which are generally agreed to be closely allied.

ARACEAE (ARUM FAMILY)

Tuberous or rhizomatous, terrestrial or aquatic (rarely floating) herbs with watery, milky or acrid sap. Leaves simple or compound, basal and solitary or clustered, or cauline and alternate. Inflorescence a spadix (an axis with small, sessile, tightly grouped flowers), subtended by an herbaceous spathe (or spathe absent). Flowers bisexual, with a perianth (in ours), or unisexual, without a perianth (the plants then monoecious or dioecious); perianth, when present, of 2-6 parts; stamens 1-6, free or united into a synandrium; gynoecium completely syncarpous, the ovary 1(-many)-locular, superior or inferior (i.e., embedded in the spadix); ovules 1-many in each locule. Fruit usually a berry. Seeds with or without endosperm, the embryo large. (Including Pistiaceae.)

A large family, primarily tropical or subtropical in its distribution, of over 100 genera grouped into eight subfamilies by Engler (18 tribes by

¹ Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation, and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. The scheme follows that outlined at the beginning of the series (*Jour. Arnold Arb.* 39: 296-346. 1958). Other published portions of these studies will be found in *Jour. Arnold Arb.* 40: 94-112, 161-171, 268-288, 369-384, 391-397, 413-419. 1959, and in the present issue. In connection with the treatments of the Araceae and the Lemnaceae, I am particularly indebted to Carroll E. Wood, Jr., for his valuable suggestions, advice, and information. The illustrations are the skillful work of Dorothy H. Marsh, and are based on material collected by Carroll E. Wood, Jr., and Richard J. Eaton. I wish also to express my indebtedness to R. B. Channell, George R. Cooley, Joseph Ewan, R. K. Godfrey, H. F. L. Rock, and Edward G. Voss, who kindly assisted in supplying information, aided in the obtaining of specimens, and helped in various other ways.

Hutchinson) with about 1500 species. Eight genera, representing five sub-families, are native to the United States, while at least two exotic genera, *Colocasia* and *Pinellia*, are becoming established. All but three of these (*Calla* L., *Lysichitum* Schott, and *Pinellia* Tenore) are represented in our area.

The family may be recognized by the inflorescence, a spadix, which usually is subtended or enveloped by a spathe. Great diversity exists with respect to the nature, position and distribution of the flowers on the spadix, the habitat, habit, leaf morphology, flower structure and other morphological characters. The subdivision of the family is based not only on floral but also on anatomical characters, such as the presence or absence of raphides and the occurrence of latex.

Although there appears to be no doubt that the family represents a natural group, much speculation exists with respect to its origin and phylogenetic relationships. Engler considered the Araceae to be derived from the Palmae through the Cyclanthaceae. Hutchinson, on the other hand, thought the group to be monophyletic and derived from the stock of the tribe Aspidistreae of the Liliaceae. Other authors have considered it as having evolved from the ancestors of the Liliaceae through various phylogenetic lines.

The Araceae as a group are notable for the occurrence of the needle-like crystals of calcium oxalate (raphides) in "packets" which occur in small capsules in almost all tissues. These account for the immunity of most Araceae to herbivorous mammals and for the intense irritation or "burning" sensation which is experienced when raw or improperly cooked corms of *Colocasia*, *Xanthosoma*, or *Arisaema* are eaten. In *Dieffenbachia*, the dumb-cane, widely grown as an ornamental foliage plant, the irritation is so severe as to produce temporary inability to speak. When the cells of the plant are broken in chewing, the capsules absorb water and the needles are discharged with sufficient force to penetrate the tissues of the mouth. The prolonged cooking which is necessary with the "edible" Araceae renders the capsules inactive. (Cf. *Colocasia*.)

Many genera are popular in cultivation as ornamentals, some, such as *Philodendron*, *Syngonium*, *Pothos*, *Scindapsus*, and *Caladium*, for their decorative foliage, others, such as *Zantedeschia* and *Anthurium*, for their showy spathes. Some of these may possibly escape sparingly in subtropical areas.

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KEY TO THE GENERA OF ARACEAE

- A. Perianth present; flowers (at least the basal) bisexual, frequently proterogynous.
 - B. Spadix lateral on a leaf-like axis; leaves sword-shaped; perianth segments 6; fruit a berry. 1. *Acorus*.
 - B. Spadix terminal on peduncle; leaves cordate, ovate, or oblong-elliptic.
 - C. Spathe fleshy, enveloping the subglobose spadix; perianth segments 4; fruit embedded in swollen spadix (multiple fruit.) 2. *Symplocarpus*.
 - C. Spathe bract-like, ensheathing base of peduncle of oblong spadix; perianth segments (in lower flowers) 6; fruit a berry, not embedded in spadix. 3. *Orontium*.
- A. Perianth wanting; flowers unisexual.
 - D. Plants rooted in soil; spadix free from spathe.
 - E. Leaves simple; stamens united into a peltate syngonium.
 - F. Leaves sagittate or hastate; spadix almost completely covered by flowers. 4. *Peltandra*.
 - F. Leaves ovate-cordate and peltate; apex of spadix naked or covered with sterile flowers; plants spreading by runners. 5. *Colocasia*.
 - E. Leaves palmately or pedately divided; stamens 2-4-locular, subsessile. 6. *Arisaema*.
 - D. Plants floating; spadix adnate to spathe. 7. *Pistia*.

Subfam. POTHOIDEAE Engl.

1. *Acorus* Linnaeus, Sp. Pl. 1: 324. 1753; Gen. Pl. ed. 5. 151. 1754.

Plant herbaceous, with a thick, creeping rhizome. Leaves equitant, sword-shaped. Spadix borne laterally on an axis resembling a foliage leaf, spathe absent (the prolongation of the fertile axis often interpreted as an open spathe). Flowers bisexual, 3-merous, greenish; perianth of 2 whorls of 3 concave tepals; stamens 6, filaments linear; gynoeceum with a 2- or 3-loculed superior ovary, each locule with several orthotropous ovules apically attached. Fruit a gelatinous, few-seeded berry. TYPE SPECIES: *Acorus Calamus* L. (*Acorus*, an ancient Latin name for an aromatic plant.) — SWEET-FLAG.

A genus of two or three species, as currently interpreted, from the northern temperate regions of the world. It is represented in our area by the widespread *Acorus americanus* Raf. which grows in low, wet areas, marshes and along the banks of quiet streams. Although generally known as *A. Calamus* and considered to have been introduced into the United States from Europe, recent cytological evidence indicates that the American plant is most likely a native one. The American plants are diploid ($2n = 24$) and fertile, while the European plants, which were introduced from southern Asia, are triploid ($2n = 36$) and sterile. Whether or not the European sterile triploid has been introduced into North America still remains to be shown. The plants of "*A. Calamus*" from Siberia and Asia are tetraploid ($2n = 48$) and fertile. Various characters have been found to be corre-

lated with the degree of polyploidy in *A. Calamus*. These include the blade width/length ratio, the angle of the spadix insertion, the oil content of the rhizome (greater with polyploidy), water content, and also the amount of calcium oxalate (decreases in polyploids). It has been suggested that each polyploid group be considered a variety of *A. Calamus*, but perhaps each might better be regarded as separate species. The American diploid (*A. americanus* Raf., *A. Calamus* var. *americanus* (Raf.) Wulff) needs further study to establish the possible validity of separation of northern and southern plants as was done by Rafinesque.

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Subfam. CALLOIDEAE Engl.

2. *Symplocarpus* Salisbury ex Nuttall, *Gen. N. Am. Pl.* 1: 105, 106. 1818, nom. cons.²

Herbs with a stout, erect rhizome bearing numerous large, clustered leaves; entire plant with a strong odor, often compared with that of a

² Conservation unnecessary; see *Taxon* 8: 230. 1959.

skunk. Leaves entire, ovate or cordate, conspicuously veined. Spathe thick, fleshy, purple spotted, ovoid, with a tapering, arched tip, the margin inrolled. Spadix ellipsoid or globose, completely covered by the crowded flowers. Flowers bisexual, proterogynous, maturing basipetally; perianth segments 4, fleshy; stamens 4, opposite the perianth segments, the filaments slender, flattened, the anthers 2-loculed, extrorse; gynoecium with a 1 (-seldom 2)-loculed ovary imbedded in the spadix, the solitary ovule pendent, orthotropous; style 4-angled, subulate. Fruits embedded in the spongy tissue of the globose spadix which is roughened by the persistent perianth parts and styles. Seeds naked, without endosperm or seedcoat, subspherical, depressed on the funicular side. (*Spathyema* Raf., nom. rejic.) TYPE SPECIES: *S. foetidus* (L.) Nutt. (Name from Greek, *symploce*, connection, and *carpos*, fruit, in allusion to the multiple fruit.) — SKUNK-CABBAGE.

Symplocarpus foetidus, is known from two widely disjunct areas: eastern Asia (the Japanese plant has been named *S. nipponicus* Makino), and eastern North America, where it ranges from Quebec and Nova Scotia, south to

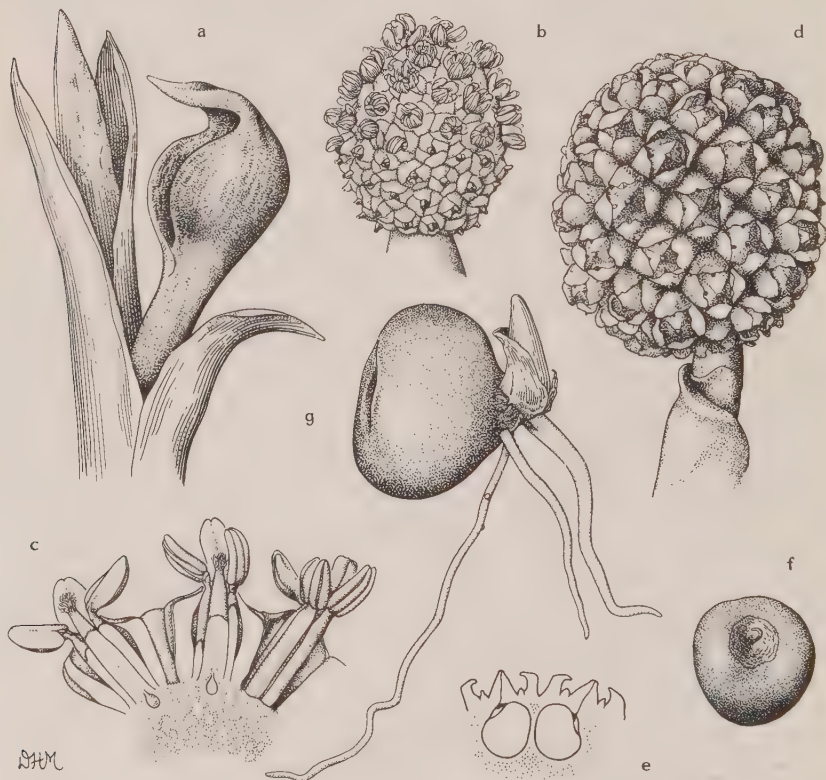


FIG. 1. *Symplocarpus*. a-g, *S. foetidus*: a, habit, showing inflorescence, $\times \frac{3}{8}$; b, spadix, $\times 1\frac{1}{2}$; c, section through spadix, showing flowers in vertical section, $\times 4$; d, fruiting spadix, $\times 1$; e, section through fruiting spadix, showing seeds in vertical section, $\times 1$; f, seed, $\times 1\frac{1}{2}$; g, seedling, $\times 2$.

New England, North Carolina, Georgia, and Tennessee and west to Ontario, northern Michigan, Minnesota, and Iowa. (It has also been recorded from Florida and Missouri.) It occurs in swamps, wet meadows, and woods, where it often forms dense stands. *Symplocarpus* is one of the earliest plants to flower in the spring. The inflorescence appears barely above the surface of the ground, long before the leaves appear. The flowers are all perfect and protogynous and mature basipetally on the inflorescence. As the embryo develops it absorbs both endosperm and integuments, so that when mature it possesses no seed coat. Except in the younger stages, during which it has a monopodial branching system, the plant is sympodial, each branch producing two leaves and a terminal inflorescence, although many of the inflorescences do not mature (Shull). The roots are contractile and function in pulling the plant into the soil.

The closest relative of *Symplocarpus* apparently is *Lysichitum*, a western American and Asiatic genus of two species, although Hutchinson, primarily on the basis of the more differentiated spathe of *Symplocarpus*, placed these two genera in different tribes. This view, however, does not seem to be supported by the morphology of the flowers, of the inflorescence, and of the vegetative body (including odor!), which are similar enough to indicate a close relationship between the two.

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3. *Orontium* Linnaeus, Sp. Pl. 1: 324. 1753; Gen. Pl. ed. 5. 151. 1754.

Perennial aquatic herbs with stout, deeply sunken rhizomes. Leaves simple, oblong-elliptic, prominently nerved and long petioled, usually floating. Spadix on an elongated scape, oblong, golden yellow, the scape green, with a band of white below the flowers. Spathe obscure, forming a sheath at the base of the scape, the blade bract-like. Flowers variable: perfect at the base of spadix, with 6 tepals, 6 stamens and a 3-carpellate gynoecium, gradually becoming staminate towards the tip; tepals yellow, 6 in two whorls to 2 in a single whorl; stamens 6-1, 1 or 2 staminodia sometimes present; gynoecium 3- or 2-carpellate; ovary 1-locular with a single basal, anatropous ovule. Fruit a 1-seeded berry with thin pericarp. TYPE AND SOLE SPECIES: *Orontium aquaticum* L. (*Orontium*, an ancient name for a plant which is said to have grown in the Syrian river Orontes.) — GOLDEN CLUB.



FIG. 2. *Orontium*. a-g, *O. aquaticum*: a, habit, $\times \frac{1}{8}$; b, spadix, $\times 1$; c, flowers, $\times 4$; d, spadix, longitudinal section, showing flowers in lateral view and in vertical section, $\times 4$; e, fruiting spadix, $\times \frac{1}{2}$; f, seed with seed coat partially removed to show embryo, $\times 2$; g, seedling, $\times 1$.

Orontium aquaticum L. is known only from the eastern United States, primarily on the Coastal Plain, where it occurs growing in the shallow water of pools or streams and on their moist banks or shores, from Florida, north to Massachusetts, and west to Louisiana and Kentucky. The flowers, which are crowded on the spadix, show a remarkable amount of variation, ranging from those with six perianth segments, six stamens and a 3-carpellate gynoecium, to those with only two perianth segments, one stamen, and one staminodium and no pistil. Numerous intermediate or transitional

conditions may also be found on the spadix. The morphological and biological details of this plant merit further investigation.

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Subfam. PHILODENDROIDEAE Engl.

4. *Peltandra* Rafinesque, *Jour. Phys. Chem.* 89: 103. 1819, nom. cons.

Herbs with long, stout-petioled, clustered leaves. Leaf blades sagittate or hastate with 3 prominent palmate nerves. Scape about as long as the petioles. Spathe convolute throughout or dilated and spreading above. Spadix completely covered with flowers, or with the apex naked. Flowers unisexual, a perianth wanting; staminate flowers covering apical portion of spadix, sessile, consisting of 4-8 two-loculed anthers embedded in the margin of a peltate shield-like scale; anthers dehiscing by terminal pores. Car-



FIG. 3. *Peltandra*. a-j, *P. virginica*: a, habit, $\times \frac{1}{8}$; b, inflorescence, $\times \frac{1}{2}$; c, spadix, basal portion, showing staminate and carpellate flowers, spathe removed, $\times 2$; d, staminate flower, lateral view, $\times 5$; e, carpellate flower, lateral view, $\times 5$; f, carpellate flower, vertical section, showing ovules, $\times 10$; g, ovule, $\times 20$; h, fruiting spadix enveloped by base of spathe, $\times \frac{1}{2}$; i, seed, $\times 2$; j, seed, apical view, seed coat partially removed to show embryo, $\times 2$.

pellate flowers covering basal portion of spadix, consisting of the 1-loculed gynoeceum surrounded by 4 or 5 white, fleshy staminodia; ovules 1-few, basal, amphitropous. Fruits 1-3-seeded berries aggregated in a fleshy head inclosed by the leathery base of the spathe; scape recurved at maturity. (*Houttinia* Necker, nom. rejic.) TYPE SPECIES: *P. undulata* Raf. = *P. virginica* (L.) Schott & Endl. (The name from Greek. *pelta*, a small shield, and *andros*, of a man, in reference to the peltiform stamens.) — ARROW-ARUM.

Three species, all of which occur in our area, of wet soils or shallow water along stream and pond borders, marshes, swamps, and wet woods in the eastern areas of North America. The best known and most widespread species is *Peltandra virginica* ($2n = c. 44, 88$), which is exceedingly variable in the shape of the blades, having seven named forms. The northern and southern extremes of this species also differ in the shape of the spathe and in the undulation of the margin of the spathe. *Peltandra sagittifolia* (Michx.) Morong (*P. glauca* (Ell.) Feay ex Wood), with an entirely white spathe and red fruits, is found from southeastern North Carolina to Florida, entirely on the Coastal Plain. The third species, *P. luteospadix* Fern., has a white-bordered spathe and yellow spadix and occurs from southeastern Virginia, southward to Florida. It has been suggested that *P. luteospadix* may have arisen as a hybrid of *P. virginica* and *P. sagittifolia* but no investigations have been made either to confirm or refute this hypothesis.

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Subfam. COLOCASIOIDEAE Engl.

5. *Colocasia* Schott, Meletemata Bot. 18. 1832.

Perennial herbs with starch-filled corms and tubers. Leaves ovate-cordate and peltate, dark velvety green above. Plants monoecious; inflorescence

stoutly peduncled, shorter than the petioles; spathe ovate-lanceolate, constricted below the middle; the spadix inclosed by the spathe, with pistillate flowers on the basal portion and staminate flowers above, the two groups separated by a group of sterile flowers, the terminal portion of the spadix naked (or covered by sterile flowers). Perianth wanting. Staminate flowers of several stamens united into a peltate body, the anthers elongate, laterally adnate or partially free and pendent, dehiscent by an apical slit. Carpellate flowers consisting of the short-styled gynoeceum, the ovary 1-locular, with numerous orthotropous ovules on the ovary wall. Fruit a berry. TYPE SPECIES: *Colocasia antiquorum* (L.) Schott, *C. esculenta* (L.) Schott, or *C. acris* (R. Br.) Schott, a lectotype apparently not yet chosen. (An old Greek name derived from the Arabic *colcas* or *culcas*.) — DASHEEN, TARO.

A genus of tropical Asiatic herbs, variously interpreted as consisting of seven or more species. *Colocasia esculenta* (L.) Schott is widely cultivated throughout the tropics for its starchy, edible tuber. Numerous cultivars occur, and several have been introduced into the United States, where the species has been grown in the lowlands of the Coastal Plain from South Carolina to eastern Texas. *Colocasia esculenta* var. *aquaticilis* Hasskarl has escaped cultivation and is an aggressive weed which forms large clones spreading vegetatively by slender, rapidly growing stolons. This plant has been poorly collected in the southeastern United States, and herbarium material is rare. It has been reported to be spreading in southern Louisiana, and it is known also from several localities from central to southern Florida growing along streams, marshes, and roadsides. The leaves of naturalized plants observed in southern Florida have a purple centrum and a purple band at the summit of the petiole. No flowering material of this form has been collected in our area. Other clones may well occur, however, and a form lacking purple markings, locally naturalized at Tallahassee, Florida, flowers in September and October (Godfrey).³

Care must be taken to cook the starchy corm thoroughly before it is eaten. Small capsules containing calcium oxalate raphides are found in abundance in all tissues of the plant. If improperly cooked, the capsules discharge the raphides with such force that they penetrate the tissues of the mouth causing great irritation. Prolonged cooking renders the capsules inactive.

³ A plant grown from a corm collected in Dade County, Florida, in May, 1958, flowered in the greenhouse at the Arnold Arboretum on October 28, 1959. The firm, fleshy spathe was 28 cm. long and light orange in color, except for the green basal portion inclosing the carpellate region of the spadix. The erect, cream-colored staminate region and the sterile appendix of the spadix were exerted from the spathe which was inclined backward above the carpellate region at an angle of about 45 degrees and which was open for about 10 cm. between this and the strongly convoluted terminal 18 cm. Flowering lasted two days: the carpellate flowers were receptive the first day and the pollen was shed on the second. The leaves of these plants bore purple markings when collected, but those produced in the greenhouse lacked this coloring.

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Subfam. AROIDEAE Engl.

6. *Arisaema* Martius, *Flora* **14**: 459. 1831.

Perennial herbs with globose or subglobose corms each bearing a simple scape sheathed by the leaf petioles. Leaves palmately or pedately divided. Spathe convolute below, spreading and arched above. Spadix obovoid and fertile at the base, above sterile (appendix) and cylindric, clavate or long attenuate. Plants dioecious or at times monoecious with both staminate and carpellate flowers in an inflorescence. Flowers without a perianth. Staminate flowers of numerous 2–4-locular, subsessile anthers opening by a slit or a pore. Carpellate flowers consisting of a gynoeceium with a uni-locular ovary containing 5 or 6 erect, orthotropous ovules. Fruits 1-few-seeded red berries, few to many borne on the enlarged, ovoid base of the spadix. (Including *Muricauda* Small). TYPE SPECIES: *A. nepenthoides* Mart. (Name from Greek, *aris*, an ancient plant name, and *haima*, blood, in reference to the red-spotted leaves of some species.) — JACK-IN-THE-PULPIT, INDIAN TURNIP.

A genus of over 100 species in 15 sections, of eastern Asia, Africa (Ethiopia), North and Central America; represented in our area by three to five species in two sections.

Section TORTUOSA Engl., with seven eastern Asiatic and one eastern American and Mexican species, is represented in our flora by *A. Dracontium* (L.) Schott ($2n = 28, 56$), green dragon or dragon root, widespread from Florida to Texas, north to southern Quebec and Ontario, and also

with disjunct stations in eastern Mexico. The pedately divided leaves and the long-exserted, slender, tapering appendix are characteristic.

Our other species belong to sect. *PISTILLATA* Engl., which includes about eight species of eastern Asia and three or four of eastern North America. The species of this section have a distinctly stipitate appendix which is more or less cylindrical and shorter than the spathe. *Arisaema quinatum* (Nutt.) Schott ($2n = 28$), of rich woods from Florida north to North Carolina and west to Louisiana, is a well-marked plant with a curved spadix and leaves generally with five leaflets. *Arisaema Stewardsonii* Britton ($2n = 28$), with the back of the spathe fluted, occurs primarily to the north of our area (Nova Scotia and southern Quebec, southward along the Appalachians at higher elevations in cold, wet woods) reaching its



FIG. 4. *Arisaema*. a-j, *A. atrorubens*: a, habit, $\times \frac{1}{8}$; b, spathe, apical view, $\times \frac{1}{2}$; c, staminate inflorescence, spathe removed, $\times 1$; d, portion of staminate spadix, $\times 6$; e, staminate flower, lateral view, $\times 8$; f, carpellate inflorescence, spathe removed, $\times 1$; g, carpellate flower, vertical section, showing ovules, $\times 8$; h, ovule, $\times 20$; i, fruiting spadix, unusually large, $\times \frac{1}{2}$; j, fruit, vertical section, showing seed, $\times 2$. k-m, *A. Stewardsonii*: k, inflorescence, lateral view, $\times \frac{1}{2}$; l, inflorescence, back view, $\times \frac{1}{2}$; m, spathe, apical view, $\times \frac{1}{2}$. n, *A. Dracontium*: habit, $\times \frac{1}{8}$.

southern limit in western North Carolina. Most of the taxonomic difficulties in the genus in our area center around the widespread *A. atrorubens* (Ait.) Blume (*A. triphyllum* sensu Huttleston) ($2n = 28, 56$), a plant primarily of woodlands in the northeastern United States, southward to South Carolina and Tennessee, and its close relatives. The status of this familiar and abundant plant and that of the smaller, later-flowering *A. triphyllum* (L.) Schott (*A. triphyllum* subsp. *pusillum* (Peck) Huttleston) ($2n = 28$) are still unsettled. Although the two are quite distinctive in some areas, in others forms of intermediate morphology occur; *A. acuminatum* Small, of the southeastern Coastal Plain, is perhaps one of these latter.

All of these species have been distinguished on morphological grounds and, for the most part, appear to be distinct ecologically. In instances in which *Arisaema atrorubens* and *A. Stewardsonii* come in contact (to the north of our range), hybrid colonies may occur. Such local hybridization and intergradation has led to the interpretation of the latter as a subspecies of the former. However, with local exceptions, these plants appear to represent distinct groups which maintain themselves as natural units.

Further careful population studies are essential. Collectors should note conformation (especially fluting of *A. Stewardsonii*), coloration and markings of the spathe, width of flange at the upper margin of the spathe, and diameter of fruits. Careful notes on habitat, flowering time, and variability of colonies should be taken.

Apart from the differing taxonomic interpretation, the nomenclatural application of the name *A. triphyllum* L. has been a matter of controversy. It is used here in the sense of Fernald (1940) for the plant formerly known as *A. pusillum* Peck; almost all literature references to *A. triphyllum* prior to 1940 apply to the plant here called *A. atrorubens*.

Numerous morphological studies have been made of *A. atrorubens* (mostly as *A. triphyllum*) and *A. Dracontium*. The factors influencing the sex of the flowers in the inflorescence of *A. atrorubens* apparently are environmental or nutritional. By manipulating the growth conditions it is possible to control the sex of the flowers that will be produced. Thus, in rich soil with an abundant water supply, carpellate flowers are produced, while staminate flowers are produced with the reduction of the root system and leaf surface of the plant.

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Subfam. PISTIOIDEAE Engl.

7. *Pistia* Linnaeus, Sp. Pl. 2: 963. 1753; Gen. Pl. ed. 5. 411. 1754.

Floating, aquatic, stoloniferous herb with a short stem bearing a rosette of leaves and numerous branching, adventitious roots. Leaves sessile, with simple, ovate to obovate-cuneate, densely pubescent blades, 3-15 cm. long,

each surrounded at its base by a membranous sheath. Spathe 2–4 cm. long, tubular at its base, but free and spreading above, slightly constricted above the middle. Plants monoecious, the spadix both staminate and carpellate; spadix fused to the median line of the spathe, free at its distal end. Flowers without a perianth, the carpellate solitary on the lower part of the spadix, the staminate whorled above; stamens 2–8, appearing to terminate the spadix. Staminate flowers subtended by a membranous collar surrounding the free portion of the spadix, this in turn subtended by a short-stalked, cordate, membranous flap. Gynoecium 1-carpellate with a 1-locular ovary containing numerous orthotropous ovules. Fruit green, ovoid to ellipsoid, many-seeded, crowned by the persistent style. Seed with a rugose, thick testa, a minute embryo, and abundant endosperm. TYPE AND SOLE SPECIES: *P. Stratiotes* L. (Generic name from Greek, *pistos*, liquid, in reference to the aquatic habitat.) — WATER-LETTUCE.



FIG. 5. *Pistia*. a-g, *P. Stratiotes*: a, habit, $\times \frac{1}{2}$; b, inflorescence, $\times 3$; c, inflorescence, lateral view, portion of spathe removed, $\times 3$; d, gynoecium, vertical section, showing ovules, $\times 4$; e, ovule, $\times 12$; f, mature fruit, $\times 3$; g, seed, $\times 6$.

A genus of a single species, *Pistia Stratiotes* L. ($2n = 28$), found floating in ponds and streams of tropical and subtropical Africa, Asia, and America. In our area it occurs in Florida and the Gulf States where it frequently forms dense mats on the water. *Pistia* is of considerable biological importance not only because of its weedy nature, which frequently results in the clogging of waterways, but also because it may represent the evolutionary line through which the Lemnaceae developed. The embryo-sac development is of the *Polygonum* (normal) type.

At least in Florida, *Pistia* does not seem to produce seeds, although the ovary tends to enlarge and to become somewhat inflated. When the plant is pollinated artificially, seeds and fruit develop normally. Whether the failure of seed development is a result of the absence of suitable pollinating agents must still be established, but the evidence at present seems to favor such an interpretation.

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LEMNACEAE (DUCKWEED FAMILY)

Small aquatic plants, floating on or below the surface of the water, consisting of a highly reduced, fleshy or membranaceous plant body (frond), lacking distinct stems and leaves, and either rootless or with one or many roots. Plants monoecious, the flowers borne in marginal pouches or in pouches on the upper surface of the frond. Staminate flower consisting of a single stamen, borne singly or in pairs; anther 2-locular. Carpellate flowers solitary, consisting of a single carpel; ovary 1-locular with 1 or 2 basal ovules. Fruit a 1- or 2-seeded utricle.

This family, generally considered to be composed of four genera and 26 species, is distributed in streams and other bodies of fresh water in most parts of the world. All four genera occur in our area and are represented by a total of 11 species which are of considerable economic and biological importance. Species of the Lemnaceae have been reported to serve as an important food for wild fowl, marsh birds, and aquatic animals, such as fish and snails.

The small plant body of the Lemnaceae is oval or elongate, and bears at its basal margin one or two reproductive pouches where the buds (and in two genera the flowers) develop. Reproduction is primarily vegetative; a single plant may multiply to several million in one season. It has been

estimated that compact floating mats of *Spirodela* contain from 100,000 to 200,000 plants per square yard of water, and mats of *Lemna* 300,000 to 800,000 plants, while those of *Wolffia* may have 1,000,000 to 2,000,000 plants per square yard.

It is generally accepted that the Lemnaceae represent a group derived from the Araceae and that the genera exhibit a reduction and simplification series from *Spirodela* to *Lemna* to *Wolffiella* and *Wolffia*. Lawalrée, however, considered the Lemnaceae to be related to the Helobiales with a close affinity to the Najadaceae.

The frond of the Lemnaceae has been interpreted as a stem functioning as a leaf, as a modified leaf, and as a structure partly foliar and partly axial. Arber compared the structure of *Pistia* with that of *Spirodela* and considered the lemaceous frond to be axial at the base and foliar at the distal region. She interpreted the distal part of the frond as a "petiolar phyllode," and considered the pockets of *Spirodela* on the lower side as being formed by "wings of the leaf-sheath, terminating in two minute ligular flaps" and on the upper side by the axis. A somewhat different point of view was expressed by Brooks who interpreted the plant body of *Spirodela* as a single sympodial branch bearing a prophyllum, a leaf, and a bract and terminating in an inflorescence, all somewhat reduced and fused to each other.

In the fall, modified fronds or "bulblets" (turions) are produced which sink to the bottom of the water where they overwinter, rise again in the spring, and begin to grow. These bulblets may also be produced during other unfavorable growth periods.

The flowers of *Spirodela* and *Lemna* are enclosed in a membranaceous spathe within the reproductive pouch. This spathe is absent in *Wolffia* and *Wolffiella*. The flowers of a single plant mature at different times. When two staminate flowers and a carpellate flower are produced by the plant the sequence of their maturation is basipetal: the distal stamen matures first, then the carpel, and finally the second stamen. This difference in the time of the maturation of the flowers doubtless promotes cross pollination. Apparently pollination may result from direct contact of the flowers as the plants float and also by the agency of insects and other small aquatic animals which are associated with these plants. The pollen grains are spherical, monocolpate and generally have spiny projections on the exine. These grains show some characters in common with certain types of the Araceae, while they are less similar to those of the Najadaceae.

The ovule is bitegmic and the inner integument forms the operculum, which persists, resembling a stopper at the micropylar end of the seed. The endosperm is cellular and forms a chalazal haustorial process, the "caecum." The monocotyledonous embryo has a short suspensor and, in some genera, lacks a radicle.

These genera have been the subject of numerous laboratory experiments dealing with the physiology of flowering and the effects of minerals, light, temperature and other factors on growth and development. Very few physiological races have been found to be present within the Lemnaceae. The small number of races has been interpreted to be a result of the mor-

phological specialization and antiquity of the Lemnaceae, their extreme reduction, and their ability to reproduce vegetatively.

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KEY TO THE GENERA OF LEMNACEAE

- A. Plant with 2 marginal reproductive pouches; segments with 1-many roots; inflorescence of 2 staminate and 1 carpellate flower surrounded by a membranaceous spathe.

- B. Fronds with 2 or more roots; conspicuously 5–18 nerved. 1. *Spirodela*.
 B. Fronds bearing a single root; obscurely 1–3 nerved. 2. *Lemna*.
 A. Plant with a single marginal reproductive pouch; segments rootless; inflorescence of 1 staminate and 1 carpellate flower without a spathe.
 C. Frond elongate, thin; stipe-attachment on one side of the reproductive pouch. 3. *Wolffiella*.
 C. Frond ellipsoid or ovoid, thick; stipe-attachment within reproductive pouch (not evident). 4. *Wolffia*.

1. *Spirodela* Schleiden, Linnaea 13: 391. 1839.

Plants solitary or in groups of 2–5. Frond round or obovate, thick, purple beneath and green above with 5–18 palmately arranged nerves radiating from the node (centrum). Roots 2–16 to each frond. Each frond with 2 marginal reproductive pouches at the basal region. Inflorescence of 1 carpellate and 2 (rarely 3) staminate flowers, inclosed within a membranaceous spathe. Stamens 2-locular, dehiscing longitudinally. Gynoecium with a 1-locular ovary and 1 campylotropous or 2 anatropous ovules. Utricle with winged margins. TYPE SPECIES: *S. polyrhiza* (L.) Schleid. (Name from Greek, *speira*, a cord, and *delos*, evident, alluding to the conspicuous roots.)

A genus of three species, represented throughout our area by *S. polyrhiza* ($2n = 40$) in aquatic habitats. While *Spirodela* is one of the most abundant and widely distributed of the Lemnaceae it seldom occurs in pure stands but is usually found growing in association with species of *Lemna* and *Wolffia*. *Spirodela oligorrhiza* (Kurtz) Hegelm. has been reported from two collections in Missouri and may possibly be found to occur in our area. It has oblong or narrowly obovate fronds with only four to six nerves and two or three (rarely more) roots.

Spirodela, the least reduced of the Lemnaceae, frequently has been compared to *Pistia*, of the Araceae.

Jacobs, in a morphological study of *Spirodela polyrhiza*, interpreted the lower flap of the reproductive pouch as "bracts which were derived by phylogenetic reduction from leaves." The plant was considered to be a "greatly reduced type of rosette in which the vertical axis has been reduced to three highly compacted nodes." Brooks has shown that the flowers of the plant are always produced in the larger, usually left-hand reproductive pouch, while the smaller, right-hand reproductive pouch produces only vegetative buds. This led him to interpret the right-hand pouch as being formed by the prophyllum and the basal part of the foliage leaf, and the left-hand, flowering pouch by the bract and foliage leaf. Occasional plants may be found, however, in which this arrangement is reversed.

The embryo sac was described by Brooks as being of the "Polygonum" (normal) type. This is the same type found in *Pistia* but differs from the other known types in the Lemnaceae, all of which are bisporic and of the "Allium" type. However, in contrast to *Pistia*, which forms four megaspores, three of which disintegrate, *Spirodela* forms two megaspores and one dyad cell; the dyad and one megaspore degenerate. The mature ovule is

campylotropous when only one is present in the ovary; when two are present they are almost completely anatropous.

In addition to its possession of numerous roots, *Spirodela* differs from the other genera of the Lemnaceae by the presence of vascular tissue in the roots, the formation of two ovules in the ovary (*L. gibba* L. is described as having as many as 7 ovules), and by the "Polygonum" type of development of the embryo sac. Brooks reports the presence of a root in the embryo of *Spirodela*, but this needs confirmation, since *Lemna* has recently been shown not to form one during its development within the seed.

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2. *Lemna* Linnaeus, *Sp. Pl.* 2: 970. 1753; *Gen. Pl.* ed. 5. 417. 1754.

Fronds solitary or in groups of 2-5, each frond with 1-3 nerves and a single root without vascular tissue. Marginal reproductive pouches 2, of unequal size, at the basal region of each frond, the flowers, when produced, always appearing in the smaller pouch, the vegetative buds in both. Inflorescence of 1 carpellate and 2 staminate flowers surrounded by a membranaceous spathe. Anther 2-loculed, dehiscing transversely. Gynoecium with a 1-loculed ovary and 1 campylotropous ovule. Utricle ovoid and smooth. TYPE SPECIES: *L. minor* L. (Name from Greek, *lemna*, an aquatic plant, possibly *Callitriche*, mentioned by Theophrastus.) — DUCKWEED.

A genus of about ten species, five of which occur within our area. By far the most common is *Lemna minor* L. ($2n = 40, 42$), which frequently forms dense covers over quiet waters. *Lemna trisulca* L. ($2n = 44$), although less conspicuous because it floats beneath the surface of the water, occurs almost as frequently as *L. minor*. Three other species known from our area are *L. valdiviana* Phil., *L. minima* Phil., and *L. perpusilla* Torr.

Several of the species of *Lemna* have been used extensively in physiological studies, although *L. minor* and *L. gibba* L. have been the subject of the greater number of the papers on the subject. (Reports of experiments on *L. major* Griff. refer to *Spirodela polyrrhiza*.) Recently Kandeler has been able to induce flowering in *Lemna gibba* ($2n = 64$); under controlled conditions it has a day-length requirement of 12–14 hours. (See also Hillman, 1959).

Lemna usually is described as having one to seven ovules in the ovary; Hegelmaier described *L. gibba* as possessing one to six. It appears that our species have only a single ovule per carpel, but a careful investigation of the various species should be made to determine this accurately.

During the development of the embryo sac most of the nucellus disappears, but a few cells persist as the nucellar or micropylar cap. The endosperm is cellular and has a chalazal haustorial outgrowth or "caecum." According to Maheshwari, no radicle is formed in the embryo. However, both Lawalrée and Brooks describe the development of a root in the embryo. Brooks has also shown that the embryo of *Lemna* has only one pouch, the vegetative pouch. These embryological characters of *Lemna* seem to agree much more closely with those of Araceae than with those of the Helobiales, which differ in the nature of their endosperm, the absence of a caecum, and in the absence of a nucellar or micropylar cap.

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3. *Wolffiella* Hegelmaier, Bot. Jahrb. **21**: 303. 1895.

Fronds thin, linear-attenuate or curved, solitary or in groups of several cohering generations, forming a star-shaped colony, rootless, each with a single, triangular vegetative pouch at the base from which arise the daughter fronds; each frond held to its parents by means of a “stipe.” Flowering reproductive pouch developing on the upper surface of the frond to one side of the stipe, thus resulting in a tendency toward asymmetry of the frond. Vegetative fronds floating just beneath the surface of the water, but in flowering the inflorescence-bearing portion of the frond breaking the surface. Inflorescence proterogynous and consisting of a single stamen with a 2-loculed anther and a single carpel with one orthotropous ovule, without a spathe. Utricle spherical. TYPE SPECIES: *W. oblonga* (Phil.) Hegelm. (Name a diminutive of *Wolffia*.)

A genus of about five species, primarily of the New World. It is represented in our area by *Wolffiella floridana* (J. D. Sm.) Thompson, which is known in the area from Michigan and Ontario south to Louisiana, Texas, Florida, and Mexico, and by *W. lingulata* (Hegelm.) Hegelm., which has been reported from Louisiana.

The flowers of *Wolffiella* were first found and described in *W. oblonga* (Phil.) Hegelm., from Argentina, in 1935. In 1938, flowering plants of *W. lingulata* were discovered in California, and, in 1948, a report of the discovery of the flowers of *W. floridana* was published. The flowers of the three species are remarkably similar, and their resemblance to the flowers of *Wolffia* is also striking. The flowering plants of *Wolffiella floridana* are slightly shorter, but wider and thicker at the base, than the vegetative plants. Furthermore, individuals are separated from the colonies during flowering time. Stomata are found only on the emergent portion of the frond during flowering.

The carpellate flower of both *Wolffia* and *Wolffiella* matures before the staminate flower. The position of the inflorescence and the structure of the flowers of the two genera are alike in all essential features. Thus, the primary basis for maintaining *Wolffiella* as distinct from *Wolffia* is the position of the vegetative shoot axis with respect to the vegetative pouch. In *Wolffiella* the vegetative pouch is formed on one side of the stipe which

attaches it to the parent plant, while in *Wolffia* the stipe and the bud develop on the lower side of the pouch near the apex of the cavity. *Wolffia* tends to be bilaterally symmetrical, while *Wolffiella* tends to be asymmetrical. This vegetative difference is presumably a very fundamental one in the morphology of the two genera.

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4. *Wolffia* Horkel ex Schleiden, *Linnaea* 13: 389. 1839.

Fronds solitary or in pairs, globose or ellipsoid, without roots or veins. Frond with a single funnel-shaped, basal vegetative pouch from within which arise the young fronds, which soon become detached. Inflorescence of a single stamen with a 2-loculed anther and a single carpel containing 1 orthotropous ovule. Spathe absent. Utricle spherical and smooth. (*Horkelia* Reichb., 1830, not Cham. & Schlecht., 1827; *Bruniera* Franch.; *Bruneria*, Small.) TYPE SPECIES: *W. Delilii* Schleid., not Kurtz. = *W. hyalina* (Delile) Hegel. (Name in honor of J. F. Wolff, 1788-1806, who wrote on *Lemna* in 1801.) — WATER-MEAL.

A genus of about 15 species, primarily of the tropics and subtropics, represented in our area by *W. columbiana* Karst., *W. punctata* Griseb. (2n = ca. 40), and *W. papulifera* C. H. Thompson. These are the smallest and simplest (by reduction) of the flowering plants, resembling small dots or grains floating in the water. Because of their minute size and the rarity of flowers these plants have been a subject of considerable botanical controversy. Dried, pressed plants are usually so shriveled and distorted that their natural shape is impossible to determine, with consequent taxonomic difficulties. The dots which are described for *W. punctata*, for instance, are apparent in dried material, but not in living plants. It has been recommended that plants of *Wolffia* be preserved in formalin-acetic alcohol and placed in flattened glass ampules which can be mounted on herbarium sheets.

Recent studies of the flowers and embryo development indicate that the anther is two- rather than one-loculed as has been previously reported. In *Wolffia* the carpel matures before the stamen, and pollination probably is effected through the agency of wind or rain.

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STUDIES IN ARTOCARPUS AND ALLIED GENERA, IV.
A REVISION OF ARTOCARPUS SUBGENUS PSEUDOJACA¹

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Subgenus *Pseudojaca* Trécul, Ann. Sci. Nat. Bot. III. 8: 117. 1847.

Artocarpus section *Pseudojaca* Renner, Bot. Jahrb. 39: 368. 1907.

Leaves alternate and distichous, simple, entire or nearly so; gland-hairs superficial or slightly immersed, heads 1(–6)-celled; spongy mesophyll compact, lacking resin-cells. *Stipules* small, nonamplexicaul, scars lateral or intrapetiolar. *Inflorescences* without sterile, solid, elongate perianths. *Male head*, perianths 2–4-lobed or -partite, intermediates between perianths and interfloral bracts frequently present. *Syncarp* globose or \pm lobed, fleshy, the surface smooth, or papillate from perianth apices or from the clavate heads of interfloral bracts (series *Clavati*; the heads enlarged in *A. styracifolius* to form flexuous processes).

LECTOTYPE SPECIES: *Artocarpus lakoocha* Roxb.

In discussing the classification of *Artocarpus* in the previous paper in this series (Jour. Arnold Arb. 40: 125–127. 1959) it was pointed out that a marked contrast, which is reflected in the differing taxonomic treatments adopted, exists between the two rather distinct subgenera in the range of variation exhibited by their species. Subgenus *Artocarpus*, which was revised in that paper, was divided into two sections and a number of series based on a variety of morphological characters (e.g., orientation of the embryo, structure of the pericarp and position of the style, thin-walled *vs.* hypertrophied fruiting perianths, well-developed *vs.* vestigial interfloral bracts, and, in the leaves, presence or absence of a hypodermis and the shape of its cells, and the details of the gland-hairs).

In subgenus *Pseudojaca*, a very different taxonomic pattern is found, due partly to a more reduced inflorescence structure, but also to the more restricted variation in vegetative characters and the occurrence of parallel evolution. Quantitative rather than qualitative characters have had to be used with much greater frequency than in subg. *Artocarpus*, both in distinguishing and in arranging the species. Nineteen of the twenty species

¹ The preceding papers in this series will be found in Jour. Arnold Arb. 40: 1–29; 30–37; 113–155, 298–368. 1959.

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recognized here are assigned to section *Pseudojaca*, in which the species have been divided into two series on the basis of the shape of the interfloral bracts. They have been arranged within the larger of these according to the length of the peduncles relative to the inflorescence heads and the shape of the male head, in conjunction with various other characters. There is a single anomalous species, *Artocarpus altissimus*, which appears to be referable to subg. *Pseudojaca*, but which is distinguished by the trinerved base and glandular-crenate margin of the leaves and by the deeply bifid styles. This is placed in a separate section, *Glandulifolium*, at the end of the paper and is further discussed there.

Before proceeding to a discussion of section *Pseudojaca*, some general comments will be made on characters that have been of use in distinguishing the species in this subgenus. In contrast to subg. *Artocarpus*, the internal structure of the syncarp has been found to provide characters of taxonomic significance only at the specific level. The fusion of the proximal regions of the perianths, the clear differentiation of an endocarp (as opposed to the induration of the entire pericarp wall), and the development of fleshy fruiting perianths (slight as compared with subg. *Artocarpus*) may distinguish apparently allied species. However, with one exception, only the first of these characters is taken into account in this discussion since evidence is still inadequate concerning the others. It is probable that a larger number of species have somewhat fleshy fruiting perianths than is recorded here, since these can only be recognized in very well preserved syncarps. External characters of the female inflorescence are of considerable value in providing specific distinctions (as in subg. *Artocarpus*). These include whether the surface is smooth or papillate at anthesis and maturity, the degree of exsertion of the styles, and whether or not the syncarp is lobed.

The leaves also differ markedly from those of subg. *Artocarpus* in being rather uniform in their internal structure and in the details of the gland-hairs. However, the characters of the indumentum are of considerable taxonomic value, though once more primarily at the specific level. The hairs on the leaves and twigs may be straight, undulate or crisped, with either smooth or rough walls. In some species a varying proportion are rather stout, smooth-walled and hooked at the tip, and the presence of such hairs can be of assistance in identifying sterile material. In general, the hairs on the leaves are restricted almost entirely to the venation, and the prominence of the latter on the lower surface of the leaf is correlated with the density of the indumentum. However, in two of the species with prominent, pubescent venation, and in three others having the venation not or slightly prominent beneath and subglabrous, nearly all the cells on the areolae on the lower surface may bear crisped hairs. The minute tomentum which is thus produced causes the leaves to appear glaucous beneath and seems to have been developed independently at least twice within the subgenus. There are six taxa in which the leaves are consistently glabrous or nearly so, and in five of these (*A. gomezianus* ssp. *gomezianus*, *A. rubrovenius*, *A. nitidus*, *A. vrieseanus* var. *subsessilis* and *A. xantho-*

carpus) a prominent reticulum is also lacking. With the exception of the last two, however, the similarity of the leaves in this respect is not, apparently, an indication of close taxonomic affinity. In *A. reticulatus* the subglabrous venation is acutely prominent beneath.

The male inflorescences have been found to be of value in indicating wider affinities with the subgenus, but, unlike the female inflorescences, they quite often fail to provide satisfactory distinctions between the species. There is usually a characteristic shape for each species, but the variation in size may be considerable, so that the dimensions in allied species overlap. Specimens bearing male inflorescences, especially if immature, must often, therefore, be identified primarily by the use of vegetative characters, whereas specimens bearing female heads at any stage from anthesis to maturity usually can be identified chiefly on their characteristics.

The species have been delimited primarily on the basis of inflorescence characters, and, in nearly all, one or more collections have been seen bearing both male and female inflorescences, enabling the characters to be correlated with certainty. However, since so many of the collections bear inflorescences of one sex only, or are sterile, vegetative characters have been of considerable practical importance in assigning material to the species recognized. (It may be remarked that the matching of collections on vegetative characters was equally necessary in subg. *Artocarpus*, although the more clear-cut specific distinctions made the proceeding less critical.)

In spite of the rather minor differences between some of the taxa in the characters of the leaves and twigs, it is possible to identify nearly all of the collections with male inflorescences and the majority of sterile collections. While this is partly a question of becoming familiar with the group, there are usually definable distinctions, and these are pointed out in notes to the species. For the purpose of identifying specimens on vegetative characters, subg. *Pseudojaca* may be divided artificially into three groups of species characteristically having "pubescent," "glabrous" and "glaucous" leaves respectively. (Two species have subspecific taxa in both "pubescent" and "glabrous" groups, and in at least two of the "pubescent" species the leaves may also be glaucous beneath). The majority of the specimens can be assigned readily to one of these groups, and the notes give the distinguishing characters for all the species in the appropriate group that have overlapping ranges.²

The two series recognized in section *Pseudojaca* are distinguished on the basis of a difference in the shape of the heads of the stalked interfloral bracts. Most of the species have bracts with peltate, discoid, ciliate heads, and are placed in series *Peltati*. There are, however, three species occurring in northern Indochina and southern China, in which the bracts have clavate or spatulate heads. These are assigned to series *Clavati*, which is further

² Notes on "pubescent" species will be found for India under *Artocarpus gomezi-anus* ssp. *zeylanicus* (31), for southeast Asia under *A. tonkinensis* (30), for western Malaysia under *A. dadah* (32), *A. fulvicortex* (40) and *A. tomentosulus* (41), and for the Philippines and eastern Malaysia under *A. vrieseanus* (33) and *A. fretessii* (35); notes on "glabrous" species are given under *A. nitidus* (43) and on "glaucous" species under *A. hypargyreus* (45).

distinguished by a small but significant difference in the length of the anthers, these measuring 0.3–0.5 mm., as compared with 0.15–0.2 mm. in series *Peltati*. The dense pubescence on the bracts gives the surface of the male head a characteristic appearance; in series *Peltati* the surface is not conspicuously pubescent and the discoid heads of the bracts can be distinguished under the binocular microscope. In two of the species in series *Clavati*, *Artocarpus hypargyreus* and *A. petelotii*, the heads of the bracts form papillae on the surface of the syncarp (not to be confused with the papillate apices of the perianths found in some members of series *Peltati*), but in the third, *A. styracifolius*, they are enlarged to form numerous flexuous, cylindric processes. The proximal region of the perianths is free in *A. hypargyreus*, partially fused in *A. petelotii* and completely fused in *A. styracifolius*. However, in spite of the very distinctive syncarp, this last species shows a relationship to *A. hypargyreus* in having leaves that are tomentulose on the areolae and hence glaucous beneath, with subglabrous main veins. In *A. petelotii*, on the other hand, the leaves are similar to those of most pubescent-leaved members of series *Peltati* in having the venation pubescent beneath, but the areolae glabrous.

In series *Peltati*, as already indicated, it has been found that the most "natural" arrangement of the species apparently can be achieved by subdividing them according to the relative length of the head and the peduncle in the inflorescences at anthesis. The sixteen species then fall into two groups, in the first of which the peduncle is nearly always as long as, or longer than the head, and in the second of which it is less than half the length of the head, at least in the male inflorescence. The length of the peduncle in the female inflorescence seems to be inherently more variable than in the male inflorescence. Its relationship to the size of the head does not, in any case, hold beyond anthesis, owing to the enlargement of the latter as the syncarp matures, although the absolute length of the peduncle is usually greater in the first group. In this group, four pairs of species can be recognized (defined by a combination of characters), but their interrelationships are not clear, and there are also two species showing reticulate alliances. The order adopted for the species is, in consequence, partly one of convenience. In the second group, the six species can again be assigned to three pairs showing a more or less close affinity to each other. An informal review of series *Peltati*, which is intended to indicate the type of variation that is found, and the reasons for the arrangement adopted, follows.

In the first group of species, *Artocarpus longifolius* (Borneo) and *A. ovatus* (Philippine Islands) are distinguished by the long-pedunculate, rather small syncarps, the usually narrowly obovoid male head and the relatively narrow, pubescent leaves with short petioles. The syncarp has the perianths completely fused in *A. longifolius*, but free proximally in *A. ovatus*, and in the latter there are abundant persistent bracts on the surface. Except for *A. tonkinensis* the remaining species have globose or pulvinate to short-obovoid male heads often overlapping in size and shape in the different species.

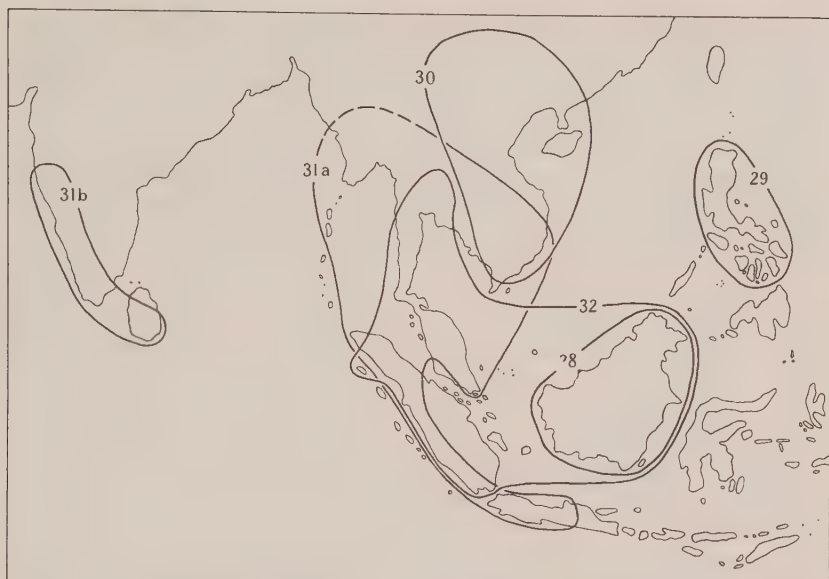


FIG. 17. Distribution of some species of subg. PSEUDOJACA. 28, *Artocarpus longifolius*; 29, *A. ovatus*; 30, *A. tonkinensis*; 31, *A. gomezianus*, a, ssp. *gomezianus* (omitting records from Assam and Cagayan Sulu), b, ssp. *zeylanicus*; 32, *A. dadah*.

The next pair of species consists of *A. gomezianus* (ssp. *gomezianus* from Burma and Indochina to western Malaysia, and ssp. *zeylanicus* in southern India and Ceylon) and *A. dadah* (Siam, Tenasserim and western Malaysia), both of which have smooth, globose syncarps with few or no interfloral bracts and free, fleshy fruiting perianths. The former is a species of monsoon regions and the latter chiefly of everwet forests, so that they are distributed differently in western Malaysia. *Artocarpus dadah* is also distinguished from ssp. *gomezianus* by having pubescent, not glabrous leaves, and from ssp. *zeylanicus* by the colour of the hairs, which are red-brown, not greyish.

Artocarpus vrieseanus (Mindanao to New Guinea and Melanesia) and *A. xanthocarpus* (northern and central Philippines) have syncarps that are very similar externally to those of the two preceding species, but are distinguished from these and the syncarps of the following species-pair by the complete fusion of the perianths. *Artocarpus vrieseanus* is a very variable species in which the proportions of the head and peduncle characteristic of this group do not always hold; of the four varieties recognized, three have more or less pubescent leaves, but one has glabrous leaves and consistently short-pedunculate inflorescences. Superficially, this species often bears a strong resemblance to *A. dadah* or to *A. fretessii*, which is placed after *A. xanthocarpus*, although it is distinguished from the former by the frequently crisped indumentum on the twigs. This similarity has deter-

mined the arrangement adopted for these species, and the syncarp character, although a convenient distinction, may not have any great taxonomic significance. *Artocarpus xanthocarpus* is superficially similar to *A. nitidus*, a species belonging to the second group, in its small, glabrous leaves and short-pedunculate male inflorescences. However, the male head is often little or no longer than the peduncle and this, with the fused perianths in the syncarp, suggests that *A. xanthocarpus* is best placed here.

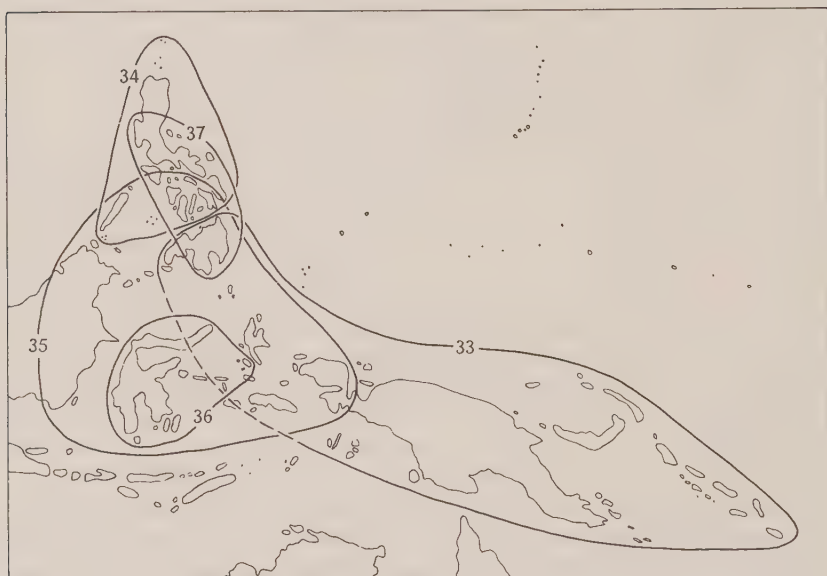


FIG. 18. Distribution of some species of subg. PSEUDOJACA. 33, *Artocarpus vrieseanus*; 34, *A. xanthocarpus*; 35, *A. fretessii*; 36, *A. reticulatus*; 37, *A. subrotundifolius*.

Artocarpus fretessii (Borneo and the Philippines to western New Guinea) and *A. reticulatus* (Celebes and Moluccas) have female inflorescences that are distinguished by being distinctly papillate at anthesis and usually strongly lobed at maturity with rather few bracts. The former has a distribution overlapping that of *A. vrieseanus* and is often difficult to distinguish when sterile, the hairs likewise being crisped on the twigs. *Artocarpus reticulatus* differs from *A. fretessii* in being larger in all its parts and in having nearly glabrous leaves which, as noted above, have an acutely prominent reticulum, unlike those of the other glabrous-leaved species.

There remain two species assigned to this group which show reticulate interrelationships. *Artocarpus tonkinensis* (Indochina and southern China) is placed after *A. longifolius* and *A. ovatus*, since it resembles both in having a relatively narrow, obovoid or ellipsoid male head and the latter in having numerous persistent bracts on the syncarp. It differs from these species, however, in having crisped hairs, as in *A. vrieseanus* and *A. fretessii*. The

perianths are fused in the syncarp, and the leaves have fewer lateral veins than in any other species of this group. *Artocarpus subrotundifolius* (Philippine Islands), which is placed last in this group, does not show any very clear alliances with the other members. The length of the peduncles, although exceedingly variable, as is the size of the very large male head, suggests that the species should be placed in this group; it also resembles *A. fretessii* and *A. reticulatus* in having a distinctly papillate female head at anthesis, with the perianths free proximally, although the syncarp is only shallowly lobed and the indumentum of the twig is patent. However, in all these characters, and in the long-exserted styles (also found, however, in *A. reticulatus*) and the broad, long-petiolate, pubescent leaves, often with an oblique base, it also resembles *A. lakoocha*, placed first in the following group of species.

The species of the second group may be characterized by the consistently short male peduncle and show no obvious alliances with members of the first group, with the exception of *A. subrotundifolius*. There is a considerable range of variation and, unlike the members of the first group, the species are most readily defined on characters of the male inflorescences and the vegetative parts, although syncarp characters can also be used.

The first four species have rather large, broad leaves, with long petioles and an often oblique base, but fall into two quite distinct pairs. *Artocarpus lakoocha* (India to Indochina and Yunnan) and *A. rubrovenius* (Philippine Islands) both have rather large, obovoid to clavate (rarely ellipsoid) male heads, but differ considerably in their leaves, those of the former being pubescent on the prominent reticulum, and those of the latter being glabrous, without a prominent reticulum. The second pair of species, *A. fulvicortex* (Malaya and Sumatra) and *A. tomentosulus* (Borneo), both of which are newly described, are distinguished from the other pubescent-leaved members of subgenus *Pseudojaca* by having the areolae on the lower surface, between the markedly prominent, pubescent reticulum, frequently tomentulose, and by the twigs being merely puberulent when young. They also differ from the other species of this second group in having globose male heads, but, whereas the syncarps in *A. fulvicortex* are subsessile, like the male heads, in *A. tomentosulus* the single syncarp seen has a peduncle 25 mm. long. In the former the syncarp has completely fused perianths; in the latter the structure is unknown, but in the remaining species of this group the perianths are free proximally.

Finally, *Artocarpus glaucus* (western Malaysia) and *A. nitidus* (Assam to southern China, western Malaysia and the Philippines), have obovoid, clavate or cylindric male heads rather smaller than in the first pair of species, and leaves that are also smaller with shorter petioles. *Artocarpus glaucus* is distinguished by the very long, narrow male head, and, as the name suggests, by the leaves, which are tomentulose on the areolae beneath, while the main veins are subglabrous. Although this indumentum resembles that found in two species of series *Clavati*, there is no other indication of an alliance between these species and *A. glaucus*, nor is there any evidence of a close relationship with the preceding pair of species. The

last species in this group is *A. nitidus*, which has a smaller male head than *A. glaucus*. It is widely distributed, and five subspecies are recognized on the basis of differences in the size and indumentum of the syncarp, associated with slight, but characteristic, variations in the glabrous leaves.

The species of section *Pseudojaca* are thus separated by a variety of relatively minor characters, so that, although they are readily distinguishable (given adequate material), they require somewhat complex definition. There has also been some parallel evolution, especially, it would seem, in the loss of the indumentum, or the development of a tomentum, and in the complete fusion of the perianths in the syncarp. The distribution of some types of hairs among the species, especially between *A. fretessii* and *A. vrieseanus*, suggests the occurrence of some introgression. In view of all this it does not seem desirable to discuss in further detail interrelationships or evolutionary trends among the species, nor is it possible to define satisfactorily any supra-specific taxa beyond the two series here recognized.

The key which follows is based, as far as possible, on "natural" characters, but practical considerations have, where necessary, taken first place in its construction. It is hoped that it will make possible the identification of most collections with male or female inflorescences at any stage from anthesis to maturity. (Where a dichotomy has had to be based on the inflorescences of one sex only, the specimens bearing inflorescences of the other sex are eliminated, if possible, further on in the key under the first alternative.) For sterile specimens, or those with very young inflorescences, the use of the footnote given above as a guide to the notes on vegetative distinctions is suggested. It should perhaps be pointed out that, while the species may be classified as characteristically "pubescent," "glabrous" or "glaucous," there are sufficient inconsistencies in the first two of these groups to limit the value of this distinction in preparing the key. The numbering of the species follows on from the previous paper in this series.

KEY TO THE SPECIES OF ARTOCARPUS SUBGENUS PSEUDOJACA

1. Styles bifid; leaves glandular-crenate, base trinerved. . . . 47. *A. altissimus*.
1. Styles simple; leaves not as above.
2. Leaves densely greyish tomentulose beneath, except for the subglabrous main veins.
3. Syncarp peduncle to 5 mm.; male peduncle to 3 mm.; leaves with 8–15 pairs lateral veins. 42. *A. glaucus*.
3. Syncarp peduncle 10–50 mm.; male peduncle 5–25 mm.; leaves with 4–9 pairs lateral veins.
4. Syncarp covered with flexuous processes; male head 4–7 mm. across; leaves with lamina decurrent on petiole, reticulum not prominent beneath. 46. *A. styracifolius*.
4. Syncarp papillate; male head 10–15 mm. across; leaves cuneate at the base, not decurrent, reticulum prominent beneath. 45. *A. hypargyreus*.

2. Leaves not tomentulose beneath, *or* main veins and reticulum also patent-pubescent.
5. Peduncles in inflorescences at anthesis at least as long as the head, *or*, if shorter in the male inflorescence, at least 7 mm.; in mature syncarp at least 13 mm.³
6. Male peduncle to 3 mm., head to 7 mm. across; leaves glabrous, reticulum not prominent beneath.
 7. Styles exerted to 0.4 mm.; male head with bracts stoutly stalked; leaves rounded or auriculate at the base, not decurrent; (syncarp peduncle to 7 mm.). 33. *A. vrieseanus* var. *subsessilis*.
 7. Styles exerted to c. 1 mm.; male head with bracts slenderly stalked; leaves usually cuneate and slightly decurrent at the base; (syncarp peduncle to 11 mm.). 34. *A. xanthocarpus*.
6. Male peduncle at least 7 mm. *and/or* leaves with the reticulum prominent and usually pubescent beneath.
 8. Petiole 3–8 × 3.5–5 mm., base of leaf cuneate or auriculate; syncarp peduncle 30–60 mm.; male head obovoid, 8–20 × 5–12 mm., peduncle 12–30 mm. 28. *A. longifolius*.
 8. Petiole not so short and stout, *or* base of leaf cordate.
 9. Female head at anthesis with styles exerted to at least 1 mm. (a few usually persisting on syncarp).
 10. Styles exerted to 1–2.5 mm.; syncarp peduncle 40(?)–75 mm.; male head 25–50 × 20–35 mm.; petiole (15–)25–65 mm. 37. *A. subrotundifolius*.
 10. Styles exerted to 1–1.5 mm.; syncarp peduncle to 45 mm.; male head smaller.
 11. Leaves glabrous or scabrid-puberulent on the prominent reticulum from hooked hairs, petiole 13–25 mm.; female head verrucose from conical papillae, or lobed at maturity and smooth over the lobes, peduncle 25–45 mm.; male head c. 15 mm. across. 36. *A. reticulatus*.
 11. Leaves pubescent, without hooked hairs; female head papillate to nearly smooth.
 12. Syncarp peduncle 35–40 mm.; leaves with 7–11 pairs lateral veins; petiole to 18 mm.; surface of the male head densely pubescent from the spatulate (not peltate and discoid) heads of the bracts. 44. *A. petelotii*.
 12. Syncarp peduncle 8–25 mm.; leaves with 9–18 pairs lateral veins, petiole 15–45 mm.; (male head 12–23 × 10–18 mm., surface covered by peltate, discoid, ciliate heads of bracts, peduncle 2–5 mm.). 38. *A. lakoocha*.
9. Female head at anthesis with styles exerted to 0.7 mm. (a few usually persisting on syncarp).
13. Syncarp subglobose or shallowly lobed, numerous dis-

³ There are a few species in which the length of the peduncle in relation to that of the head is variable, or in which the proportions differ in the male and female inflorescences; these are brought down on both sides of this dichotomy, the characters of the discordant inflorescences being given in parentheses.

- coid heads of bracts persisting on surface, often completely covering head at anthesis; male head obovoid to ellipsoid, at least 8 mm. across, peduncle at least 7 mm.
14. Leaves glabrous, reticulum not prominent beneath. 31. *A. gomezianus* ssp. *gomezianus*.
 14. Leaves pubescent, reticulum distinctly prominent beneath.
 15. Petiole 15–45 mm.; (male head to 7 mm. across, peduncle to 2 mm.). 41. *A. tomentosulus*.
 15. Petiole to 15 mm.
 16. Syncarp peduncle (40–)70–80 mm., perianths free proximally; male peduncle 20–40 mm.; twigs with patent hairs; leaves with 11–20 pairs lateral veins. 29. *A. ovatus*.
 16. Syncarp peduncle 30–40(–65) mm., perianths completely fused; male peduncle 7–12 mm.; twigs with appressed and crisped hairs; leaves with 6–9 pairs lateral veins. 30. *A. tonkinensis*.
 13. Syncarp subglobose or lobed, bracts lacking at least on lobes, often nearly all deciduous before anthesis; male head pulvinate, globose or obovoid, if obovoid less than 8 mm. across.
 17. Young twigs greyish pubescent, *or*, if glabrous, leaves without prominent intercostal veins beneath. 31. *A. gomezianus*.
 17. Young twigs red-brown to yellow pubescent, *or*, if glabrous, leaves with prominent intercostal veins beneath.
 18. Syncarp with well-defined, subglobose lobes (unless many seeds are formed), the surface between papillate and often with bracts persisting, perianths free proximally; male heads to 7 mm. across, often borne on short-shoots on older wood, bracts slenderly stalked; twigs usually with subappressed and crisped hairs. 35. *A. fretessii*.
 18. Syncarp globose or shallowly lobed, bracts usually nearly all deciduous; male heads to 15 mm. across, usually in leaf-axils, bracts stoutly stalked.
 19. Syncarp yellow, subglobose and smooth, *or* (in var. *papillosus*) papillate at anthesis and often shallowly lobed at maturity, perianths completely fused; twigs usually with some or all of the hairs subappressed and crisped, varying subglabrous; larger leaves with up to 13 pairs lateral veins. 33. *A. vrieseanus*.

19. Syncarp green with pink flesh, subglobose and smooth, perianths free proximally; twigs with patent hairs; larger leaves with up to 20 pairs lateral veins. 32. *A. dadah*.
5. Peduncles in inflorescences at anthesis less than half the length of the heads, in male inflorescence to 5 mm., in mature syncarp to 12 mm.
20. Leaves glabrous, reticulum not or scarcely prominent beneath.
 21. Male head 15–45 \times 10–25 mm.; leaves often broadly elliptic to ovate, with a broad, oblique base, petiole 15–30 mm. 39. *A. rubrovenius*.
 21. Male head to 12 \times 7 mm.; petiole 5–25 mm.
 22. Female head with perianths free proximally, styles exerted to 0.5 mm.; male head obovoid, cylindric or clavate. 43. *A. nitidus*.
 22. Female head with perianths completely fused; male head short-obovoid to globose.
 23. Styles exerted to 0.4 mm.; male head with bracts stoutly stalked; leaves rounded or auriculate at the base, not decurrent. 33. *A. vrieseanus* var. *subsessilis*.
 23. Styles exerted to c. 1 mm.; male head with bracts slenderly stalked; leaves usually cuneate and slightly decurrent at the base. 34. *A. xanthocarpus*.
20. Leaves pubescent, reticulum distinctly prominent beneath.
 24. Petiole to 15 mm. 33. *A. vrieseanus*.
 24. Petiole 15–45 mm.
 25. Male head 12–25 \times 10–18 mm.; styles exerted to 1–1.5 mm.; twigs pubescent; leaves never with the intervenium tomentulose beneath. 38. *A. lakoocha*.
 25. Male head to 7 \times 6 mm.; styles exerted to 0.5 mm.; twigs subglabrous; leaves often with the intervenium tomentulose beneath.
 26. Leaves with 6–10 pairs lateral veins and few intercostals; syncarp peduncle to 5 mm. 40. *A. fulvicortex*.
 26. Leaves with 10–14 pairs lateral veins and numerous intercostals; (syncarp peduncle c. 25 mm.). 41. *A. tomentosulus*.

Section *Pseudojaca*

Folia margine non glandulifera. *Capitula feminea* stylis simplicibus.

Series *Peltati* Jarrett, ser. nov.

Inflorescentiae bracteis interfloralibus peltatis. *Capitula mascula* cellis antherum 0.15–0.2 mm. longis.

28. *Artocarpus longifolius* Becc. For. Borneo, 629. 1902, "*longifolia*." Holotype, Borneo, *Teysmann HB 11312* (FI).

Trees, height to 21 m. Twigs 4–6 mm. thick, subglabrous to densely

pubescent, hairs red-brown to yellowish, patent, straight or some longer and hooked at the tip. *Leaves* 9–33 \times 4.5–11 cm., obovate-elliptic or elliptic, with an acumen to 2 cm. long, base cuneate, often auriculate, margin entire; main veins and reticulum very prominent beneath; glabrous above except for the pubescent main veins, venation beneath pubescent, hairs colourless, straight, varying to subglabrous; lateral veins 9–14 pairs, curved; intercostals parallel; green, drying pale or reddish brown, lighter beneath, venation concolorous; petiole 3–8 mm. long, stout.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 8–20 \times 5–12 mm., obovoid; perianths of c. 3 free segments 0.4 mm. long; stamen 0.5 mm. long, filament broad, contracted above, anther-cells globose, 0.15 mm. long; bracts slenderly stalked, heads peltate, to 0.3 mm. across, these and perianths minutely pubescent; peduncle 12–30 \times 1 mm., pubescent, hairs rufous or whitish; *female head* with styles exerted to 0.2 mm. through low papillae emerging between peltate bracts. *Syncarp* (submature) 2 cm. across, ellipsoid, drying fulvous, the surface nearly smooth, very shortly pubescent, with scattered persistent bracts; proximal region of perianths fused; peduncle 30–60 \times 2–4 mm., pubescent, hairs rufous or whitish.

DISTRIBUTION: endemic to Borneo.

Borneo. SARAWAK. Kuching, *Haviland* 2189 (BM, K, SING, ♂, ♀), *Haviland & Hose* 3205 (BM, ♂ ♀), 3206 (K, ♂, ♀). WEST BORNEO. Landak, *Teysmann HB* 11312, 1875 (FI, ♂, ♀). SOUTH AND SOUTHEAST BORNEO. Puruktjahu, *bb* 11109 (BO). EAST AND NORTHEAST BORNEO. W. Kutei: near Lahum, *Endert* 1840 (L, ♂). E. Kutei: Samarinda, Blajan River, Loa Lampong, *Nedi* 769 (CGE, L, ♂, ♀).

The material of *Artocarpus longifolius* is limited and the variation in the indumentum is considerable, but the collections agree in the characters of the inflorescences and in the distinctive shape of the leaves and petioles. The large stipules (5–15 mm. long), which are frequently persistent, and the short, stout petioles are unique in subg. *Pseudojaca*. The subglabrous collections may be from saplings or sucker shoots, since the leaves and internodes are somewhat longer than in the pubescent collections. The cuneate base of the leaf and the shorter petiole, in addition to the smaller inflorescences and the completely fused perianths in the syncarp, distinguish this species from *Artocarpus ovatus*.

29. *Artocarpus ovatus* Blanco, Fl. Filip. 666. 1837, "*Arctocarpus ovata*," non Noronha, 1790 (nomen nudum), ed. 3. 3: 73. plate. 1879; Vidal, Revis. Pl. Vasc. Filip. 254. 1886; Ahern, Timber Tree Sp. Philip. 21. plate. 1901. Neotype, Luzon, *Merrill SB* 254 (BM).

Artocarpus cumingiana Tréc. Ann. Sci. Nat. Bot. III. 8: 119. t. 4, figs. 117, 118. 1847, "*Cummingiana*"; Fern.-Villar, Noviss. App. 203. 1880; Merr. Publ. Gov. Lab. Philip. 27: 80. 1905, Sp. Blancoanae, 125. 1918, Enum. Philip. Pl. 2: 40. 1923; Renner, Bot. Jahrb. 39: 370. 1907; Elmer, Leaf. Philip. Bot. 2: 620. 1909; Whitford, Bull. Bur. For. Philip. 10(2): 28. t. 6. 1911; Brown, ibid. 22(2): 70. fig. 23. 1921. Holotype, Cebu, *Cuming* 1784 (P); isotypes (BM, CGE, K).

Artocarpus acuminatissima Merr. Philip. Jour. Sci. 18: 49. 1921, Enum. Philip. Pl. 2: 40. 1923. Holotype, Luzon, *De Mesa & Rosario* FB 22777 (PNH, destroyed); isotypes (κ, us); lectotype (κ).

Trees, height to 25 m., bark brown. *Twigs* 2.5–4.5 thick, smooth or finely rugose, short-pubescent, hairs red-brown to pale yellow, patent, straight, or some longer and undulate. *Leaves* 15–33 × 6–16 cm., oblong to obovate-oblong, varying elliptic, with an acumen to 2(–4) cm. long, base cordate, varying rounded, rarely cuneate, margin entire; main veins and reticulum prominent beneath; glabrous or nearly so above except for the pubescent main veins, venation beneath thinly to densely pubescent, hairs colourless, straight or undulate, some on main veins stout and with hooked tips; lateral veins 11–20 pairs, curved, basal 2–3 pairs crowded; intercostals parallel or reticulate; deep green above, paler beneath, drying red-brown to blue-grey above, pale or reddish brown beneath, venation usually concolorous; petiole 8–15 mm. long.

Inflorescences solitary or paired in leaf-axils, the male heads also on short shoots on older wood. *At anthesis: male head* 12–32 × 10–15 mm., obovoid (rarely subglobose); perianths 2- or 3-lobed, divided nearly to the base, 0.5 mm. long; stamen 0.8 mm. long, filament flattened, tapering above, anther-cells ellipsoid, 0.15 mm. long; bracts stoutly stalked, heads peltate, to 0.4 mm. across, these and perianths sparsely ciliate; peduncle (15–)20–40 × 2 mm., indumentum as twigs; *female head* with styles exerted to 0.5 mm. through a dense covering of peltate bracts. *Syncarp* to 3 cm. across, subglobose, shallowly lobed, yellowish white, drying brown, the surface smooth, very shortly pubescent, with numerous persistent bracts; wall c. 2 mm. thick; proximal region of perianths free, fruiting perianths c. 4–6, thin-walled, “seeds” (endocarps) subellipsoid, 12 × 9 mm.; core c. 8 mm. across; peduncle (40–)70–80 × 2.5 mm., indumentum as twigs.

VERNACULAR NAMES: *cubi*, *anubing*. USES: provides a hard timber; the wood of other species of subg. *Pseudojaca* in the Philippines is sold under the same vernacular names.

DISTRIBUTION: in forests to 2500 ft.; northern and central Philippine Islands.

Philippine Islands. MINDORO. *Medina* FB 24178 (A, ♀). Mansalay: Barrio Manual, *Sulit* PNH 17175 (κ, L, PNH, ♂); Mt. Yagaw, *Conklin* PNH 17464 (κ, PNH, ♀). LUZON. *Ahern* 119 (BO, ♂ ♀), 786 (BO, ♀). Abra: Manabo, *Paraíso* FB 31103 (SING, ♂). Mountain Province: Kalinga Subprov., Lubuagan, *Celestino* PNH 7846 (A, ♂ ♀). Benguet: *Leano* FB 24712 (us, ♀). Isabela: San Mariano, *Clemens* 17032 (c), *Ramos & Edano* BS 46810 (c, SING, ♂ ♀). Nueva Viscaya: near Dupax, *McGregor* 11495 (c, SING, ♂). Zambales: Mt. Pinatubo, *Fox* PNH 4677 (PNH). Bataan: *Alambra* FB 25303 (SING, ♂). Nueva Ecija: *Alvarez* FB 22143 (L). Bulacan: Angat, *Vidal* 3841 (κ, ♀). Rizal: *Ahern* FB 2905 (BO, κ, P, SING, ♂, ♀), *Maneja* FB 23978 (A, BO, L, ♂), *Reillo* BS 15173 (BO, L, P, ♂, ♀); Antipolo, *Merrill* 1680 (κ, ♂), *SB* 254 (A, BM, BO, GH, κ, L, P, ♂); Bosoboso, *Merrill* 2822 (A, BM, κ, ♀); Montalban, *Loher* 6948 (κ, ♂); Mt. Angilog, *Lopez* FB 42035 (A, BM, κ, SING, ♂, ♀). Laguna: Los Banos, *Elmer* 8175 (BO, κ, ♂), *Holman* 93 (A, ♂); Los Banos, Mt. Makiling, *Banaga*

PNH 33385 (L, ♂), *Elmer* 18467 (A, BM, K, L, ♂), *Rivera* PNH 9481 (BM, L, PNH, ♂), *Sulit & Paa* 38 (A, ♀); Santa Maria, Maritac, *Curran* FB 10040 (BO). Tayabas: *Cailipan* FB 26019 (BO, L, ♂, ♀), *Manuel* FB 27456 (P); Ainoban, *De Mesa & Rosario* FB 22777, Sept. 1913 (K, US, ♀); Langumanoc, *Ware* FB 7 (BO, ♂, ♀); Lucban, *Elmer* 9163 (A, BO, K, L, ♂). Camarines: *Alambra* 28085 (A, ♀), *Curran* FB 10426 (BO, ♂); Mt. Bagacay, *Ramos & Edano* BS 33922 (A, K, ♂, ♀); Mt. Isarog, *Curran* FB 10444 (BO, ♂). Sorsogon: *Curran* FB 10523 (BO, ♂); Irosin, Mt. Bulusan, *Elmer* 14424 (A, BM, K, L, ♂, ♀), 14458 (A, BM, K, L, ♀). MARINDUQUE. *Rosenbluth* BS 12152 (BO, ♂). CATANDUANES. *Ramos & Edano* BS 75302 (SING, ♂, ♀). SIBUYAN. Magellanes, Mt. Giting-Giting, *Elmer* 12332 (A, BM, BO, K, L, ♂). MASBATE. *Merrill* 3078 (A, BM, K, P, ♀). TICAQ. *Vidal* 3840 (A, K, ♂). CEBU. *Cuming* 1784, 1841 (BM, CGE, K, P, ♂). NEGROS. *Cardona* FB 24219 (A, US, ♀), *Everett* 7301 (BO). Occidental: *Danao* FB 15036, *Everett* 4305 (BO, ♂); Cadiz, *Oliveros* FB 29891 (NY, ♂). Oriental: Dumaguete, Cuernos Mts., *Elmer* 9890 (A, BM, BO, K, L, ♂). PANAY. Ilo-ilo, *Vidal* 596 (K, L, ♂).

Blanco's description of *Artocarpus ovatus* is clearly identifiable, but his name was reduced by Fernandez-Villar (1880) to *A. cumingiana* Tréc. (the misspelling of which as "*cummingiana*" arose from a misprint on the labels in the Paris herbarium). Merrill (1905) also used Trécul's name since he found (presumably from "Index Kewensis") that Noronha had published an *Artocarpus ovatus* in 1790 and was unaware that the latter was a *nomen nudum*.

Artocarpus ovatus is quite distinct from the other Philippine species of subg. *Pseudojaca* in its long-pedunculate, relatively small inflorescences. Nevertheless, it has frequently been confused with *A. fretessii*. Under the latter are given characters distinguishing these two species and *A. subrotundifolius*, another pubescent-leaved species which occurs in the Philippines.

30. *Artocarpus tonkinensis* A. Chev. ex Gagnep. Bull. Soc. Bot. Fr. 73: 90. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 737. 1928; Merr. Lingnan Sci. Jour. 6: 275. 1930, 7: 303. 1931; Metcalf, Jour. Arnold Arb. 26: 198. 1945. Syntypes, Indochina, *Balansa* 2486, *Castellini* 111, *Poilane* 1859, *Service Forestier* s.n. (P); lectotype, *Poilane* 1859 P).

Artocarpus tonkinensis A. Chev. Bull. Écon. Indo-Chine 20(no. 132): 861. 1918, *nomen nudum*.

Artocarpus sp., Merr. Lingnan Sci. Jour. 5: 63. 1928.

Trees, height to 15 m. Twigs 1.5–2.5 mm. thick, reddish brown, short-pubescent or puberulent, hairs usually appressed and crisped. Leaves 9–23 × 4–10 cm., elliptic, obovate- or oblong-elliptic, or obovate-oblong, acuminate, base cuneate or rounded, margin entire; juvenile leaves with margin shallowly dentate towards apex; main veins and reticulum prominent beneath; glabrous above or the main veins puberulent, venation beneath thinly pubescent, hairs colourless and undulate; lateral veins 6–9

pairs, curved; intercostals parallel; deep green above, paler beneath, usually drying greyish green with reddish main veins and reddish or straw-coloured reticulum; petiole 4–12(–20) mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 10–25 \times 8–15 mm., obovoid to ellipsoid; perianths of 2 or 3 free segments 0.5 mm. long; stamen 0.7 mm. long, filament tapering above, anther-cells ellipsoid, 0.2 mm. long; bracts slenderly stalked, heads peltate, to 0.4 mm. across, these and perianths short-ciliate; peduncle (5–)7–12 \times 1.5 mm., velutinous; *female head* with styles exerted to 0.7 mm. through a dense covering of peltate bracts. *Syncarp* to 6.5 cm. across, subglobose, shallowly lobed, yellow, drying rufous, the surface smooth, pubescent, with scattered persistent bracts; wall 5–8 mm. thick; proximal region of perianths fused, fruiting perianths 6–12, thin-walled, “seeds” (endocarps) subellipsoid, 12–15 \times 9–12 mm.; core c. 10 mm. across; peduncle 30–40(–65) \times 2.5 mm., velutinous.

USES: cultivated for the edible fruit.

DISTRIBUTION: in forests to 4000 ft.; Indochina and southern China.

Indochina. CAMBODIA. *d'Alleizette*, 1909 (P, ♂). ANNAM. Bu Khang, near Vinh, *Poilane* 16644, 16647 (P, ♀). Thanh Hoa Prov.: Na bam, *Poilane* 1859 (K, P, ♂). TONKIN. Bac-giang Prov.: Bac le, *Serv. For.* (P, ♀). Ha-coi: Sai Wong Mo Shan, *Tsang* 30266 (A, ♂); Taai Wong Mo Shan, *Tsang* 29321 (A, ♂). Song Hoa, *Castellini* 111, Oct. 1905 (P). CHINA. YUNNAN. Szemao, *Henry* 13015 (A, K, ♂). KWEICHOW. Bua-li, Chenfeng, *Teng* 91028 (A, ♀). KWANGSI. Ping Nam Hsien, *Wang* 40423 (A, ♀). KWANTUNG. Fan Ch'eng district, Kung P'ing Shan, *Tsang* 26749 (A, ♂); Sunyi district, Sie River, *Tsiang Ying* 2677 (K, SING, ♂). HAINAN. Wang 33671 (A, P, ♂, ♀); Ching Mai district, Pak Shik Ling, *Lei* 830 (A, K, L, SING, ♀); Lai area, Hung Mo Shan, *Tsang & Fung* 295 (A, BM, K, NY, P, ♂, ♀), 661 (K, NY, US, ♂); Lam Ko district, Siu Shui Hang, Lin Fa Shan, *Tsang* 250 (A, BM, K, ♂); Ling Shui district, Chim Shan, Fan Maan Ts'uen, *Fung* 20192 (A, BM, K, NY, P, US, ♂); Lokwui, *How* 72358 (A, P, ♂); Ngai district, Chiu Sam Tsuen, *Lau* 395 (A, BM, K, P, ♂); Po-ting, *How* 72008 (A, BM, P, ♂), 72552 (A, BM), 73076 (A, P, ♂), 73252 (A, SING, ♂), 73471 (A, BM, P, ♀); Taam-chau district, Shan Tong To, *Tsang* 706 (A, BM, K, ♀); Wik Tsok Man, *McClure* 9752 (K); Yaichow, *Liang* 62632 (A, NY, US, ♀). **Cultivated.** INDOCHINA. Tonkin, Ké Sô, *Balansa* 2486, May 1886 (P, ♀). CHINA. Kwangtung, Loh Kong Tung, Taai Shaan, *McClure* 13564 (K, P).

Chevalier, in 1918, gave details of the wood only under the name *Artocarpus tonkinensis*, and this was not validly published until 1926, when Gagnepain supplied a botanical description. In the same area there are two other pubescent-leaved species with which *A. tonkinensis* might be confused. In *Artocarpus lakoocha*, the styles are exerted to 1–1.5 mm., the peduncles are shorter (the male to 5 mm., the female to 15(–25) mm.), the leaf has more numerous lateral veins (9–18 pairs), and the petiole is longer ((10–)15–45 mm.). In *A. petelotii* the interfloral bracts are clavate, and the surface of the syncarp hence more or less papillate, while the indumentum of the twigs and leaves is longer and not crisped.

31. *Artocarpus gomezianus* Wall. ex. Tréc. Ann. Sci. Nat. Bot. III. 8: 118. 1847, "*Gomeziana*"; Kurz, For. Fl. Burma 2: 433. 1877; King in Hook. f. Fl. Brit. Ind. 5: 544. 1888; King, Ann. Bot. Gard. Calcutta 2: 15. 1889, pro parte, excl. *t.* 14A et spec. King 4189, 5078, 7535, 8838, Maingay 1486 (*A. nitidus* ssp. *griffithii*) et Wallich 4658A (*Ficus callophylla* Bl.); Parkinson, For. Fl. Andaman Is. 253. 1923; Kanjilal et al. Fl. Assam 4: 269. 1940. Holotype, Burma, Wallich 4660 (c, not seen, photograph in A); isotypes (CAL, CGE, K).
Artocarpus gomeziana Wall. Cat. no. 4660. 1831, nomen nudum.
Artocarpus petiolaris Miq. Fl. Ind. Bat. Suppl. 422. 1861. Holotype, Sumatra, Teysmann HB 752 (v); isotype (bo).
Artocarpus pomiformis Teysm. & Binnend. Natuurk. Tijdschr. Ned. Ind. 25: 400. 1863; Koord. & Val. Bijdr. Boomsort. Java 11: 23. 1906; J. J. Smith, Ic. Bogor. 3: 87. *t.* 235. 1907; Backer, Beknopte Fl. Java 6: 15. 1948.
Artocarpus lakoocha Roxb. var. β *gomeziana* (Wall.) Trimen, Handb. Fl. Ceylon 4: 99. 1898, quoad nomen, non quoad plantam.
Artocarpus masticata Gagnep. Bull. Soc. Bot. Fr. 73: 88. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 739. 1928. Holotype, Annam, Poilane 5492 (p); isotypes (K, P).

ssp. *gomezianus*

Evergreen trees, height to 40 m., bark dark grey-brown. Twigs 2–4 mm. thick, smooth or finely rugose, appressed-puberulent, soon glabrescent. Leaves 11–25 \times 7–16 cm., oblong, varying to elliptic, short-acuminate, base broadly rounded, varying to cuneate or subcordate, glabrous, margin entire or shallowly crenate; main veins prominent beneath; lateral veins 10–15(–20) pairs, straight or slightly curved; intercostals parallel; deep green above, paler beneath, main veins greenish white, usually drying pale greenish or greyish brown with straw-coloured main veins; petiole 15–30 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: male head 10–25 mm. across, obovoid to subglobose; perianths 2- or 3-lobed, divided nearly to the base, 0.5 mm. long; stamen 0.6 mm. long, filament stout, abruptly contracted above, anther-cells globose, 0.2 mm. long; bracts stoutly stalked, heads narrowly peltate, to 0.4 mm. across, these and perianths with sparse, short hairs; peduncle 7–17 \times 1 mm., puberulent; female head with peltate bracts being shed or already fallen and styles exerted to 0.3 mm. through perforations in the surface. *Syncarp* to 8 cm. across, subglobose, yellow with pink flesh, drying brown or black, the surface smooth, velutinous; wall c. 8 mm. thick; proximal region of perianths free, fruiting perianths several, fleshy, "seeds" (indurated endocarps) ellipsoid, 12 \times 10 mm.; core c. 20 mm. across; peduncle 15–45 \times 8 mm., velutinous.

USES: there is one record of the fruit being edible (Poulo Condore, Harmand 700); the roots are chewed with betel (Annam, Poilane 5492).

DISTRIBUTION: in evergreen and semi-evergreen forest to 2000 ft. in regions with a distinct dry season; Assam ?, Burma, Andaman Islands, Siam, southern Indochina, Malaya, Sumatra, Java (western and central provinces), Philippine Islands (Cagayan Sulu, ? introduced).

Burma. Pinmona [? Pyinmana], *Huk*, Aug. 1890 (P, SING). TENASSERIM. Tavoy: *Wallich* 4660 (leg. *Gomez*), Nov. 1827 (CAL, CGE, K, ♂). Mergui: Victoria Point, *Po Khant* 11343 (DD, ♀). Andaman Islands. *King* 416 (K, ♀). Siam. Ko Kahdat, *Schmidt* 556 (C, ♂); Muak Tek, Sanaburi, *Kerr* 9064 (BM, ♂); Chantaburi, *Jeppeson*, May 1947 (C); Sraburi, Phu Khae, *Smitinand* 1549 (CGE). PENINSULAR SIAM. Bangtapan, *Kerr* 1436 (BM, ♀); Krabi, Ao Luk, *Kerr* 18608 (BM, ♂); Surat, Kaw Tao, *Kerr* 12700 (BM, K, L, P, ♂); Trang, Chum Het, *Kerr* 15214 (BM, K, P, ♀); Trang, Thap Tiang, *Fox* 3845 (SING, ♂, ♀). Indochina. CAMBODIA. *Béjeaud* 640 (NY, P, ♀). ANNAM. Nhatrang Prov., Phu-hu, between Nhatrang and Ninhhoa, *Poillane* 5492, Jan. 1923 (K, P, ♂). POULO CONDORE. *Harmand* 700 (P, ♀).

Malaya. Novadens Hill, *Maingay* 1486 (GH, K, L, ♂). KEDAH. Baling, *Abdullah KEP* 27356 (KEP); Kokmoi For. Res., *Hassan KEP* 42427 (KEP, ♀); P. Songsong, *Curtis*; June 1890 (P); Sik, *Mohamed KEP* 11327 (KEP, ♀). KELANTAN. Tumpat, *Corner SFN* 33529 (SING, ♂), *Ngadiman SFN* 33698 (SING, ♀). PAHANG. Bentong, Clough For. Res., *KEP* 78746 (KEP); Bentong, Ulu Benus, *Symington KEP* 51821 (KEP, ♀). JOHORE. Sungei Rhu Riba, Jason Bay, *Corner* (SING, ♂). LANKAWI ISLANDS. P. Butong, *Curtis* 906 (K, SING, ♂). PENANG. Road to Balik Pulau, *Curtis* 2462 (K, SING, ♂). SINGAPORE. *Didrichsen* 4412 (C, ♂). P. TIOMAN. Telok Paya, *Nur SFN* 21742 (BO, KEP, SING, ♂).

Sumatra. ATJEH. Seulimeum, Lam Temot, *bb* 5876 (BO, L). TAPANULI. Padang Lawas, Purbasinamba, *bb* 6186 (BO). WEST COAST. *Teysmann HB* 798 (BO, U, ♀); Baros, *Teysmann HB* 721 (L), 752 (BO, U, ♂). EAST COAST. Huta Padang Estate, near Kisarin, *Krukoff* 225 (BO, ♂). BENKULEN. Redjang, Sukamarindu, *bb* 8861 (BO); Redjang, Tabah Penandjung, *bb* 2822 (BO, L). P. WEH. Baloken, *Koorders* 10578, 10579, 10580 (BO, ♀).

Java. WEST JAVA. Buitenzorg: Djampang Kulon, Tjikankung, Tjidjaringao, *NIFS Ja* 1250 (BO, ♀). Preanger: Palabuanratu, Sukabumi, *Koorders* 8687 (BO, ♂). CENTRAL JAVA. Pekalongan: Mayasari, *Burger* 3340 (BO, ♂); Prupuk, *Wind* 26 (BO, L, ♀). Semarang: *Koorders* 9419 (BO, L); Kedungdjati, *Koorders* 8674 (BO, L), 8676 (BO, L, ♂), 8677 (BO, ♂, ♀), 8690 (BO, L, ♂), 25251 (BO, L, P, ♀), 25322, 26139 (A, BO, L), 33701 (BO, K, L, ♂, ♀); Kedungdjati, Deras, *Koorders* 8675 (BO, L, ♂, ♀), 8691, 9271, 25319 (BO, L); Kedungdjati, near Gunong Kenting, *Koorders* 24957 (BO, L, ♂); Kedungdjati, Prizi, *Koorders* 25475 (BO, L); Kedungdjati, Pungge, *Koorders* 8678 (BO, P), 8679 (BO, L); Kedungdjati, Trimze, *Koorders* 8689, 8692 (BO, L, P), 8693 (BO); Telawa, *Jansen* 4637 (BO, ♂). Jogjakarta: Zuidergebergte, *Teysmann* (BO).

Philippine Islands. CAGAYAN SULU. *Antonio FB* 30634 (NY), *Merrill* 5304 (BO, L, NY, P, US, ♂, ♀); Buluan Ranch, *Santos* 4772 (L, ♂, ♀). Cultivated. JAVA. Bogor, Hort. Bot., *HB* 7289 (BO, P), *VIII B* 41 (L).

The synonyms listed above all refer to *Artocarpus gomezianus* ssp. *gomezianus*, but the name *A. lakoocha* Roxb. var. *gomeziana* (Wall.) Trimen was used by Trimen and later authors in the sense of *A. gomezianus* ssp. *zeylanicus*.

The variety *griffithii*, based on Malayan material, which was described under *Artocarpus gomezianus* by King in 1888 and 1889, is here transferred to *A. nitidus* as a subspecies; the distinguishing characters and the confusion that has occurred between the entities in Malaya are discussed there. All other references in the literature to *A. gomezianus* as occurring

in Malaya are based on *A. nitidus* ssp. *griffithii*. *Artocarpus gomezianus* ssp. *gomezianus* is mainly restricted to the north of Malaya and the east coast, where there is a distinct dry season, although a single specimen has been seen from Singapore.

The distribution of ssp. *gomezianus* in western Malaysia is apparently somewhat discontinuous, corresponding to its climatic requirements. However, no significant variation is shown within this subspecies and the maintenance of *A. pomiformis* Teysm. & Binnend. as a distinct species in Java presumably arose from its comparison with King's description and plate, which were largely (the latter solely) based on material which should have been referred to his var. *griffithii*. The subspecies is apparently absent from Borneo and it is possible that the specimens from Cagayan Sulu were taken from a tree, or trees, that had been introduced, although there is no evidence for this. Kanjilal *et al.* (1940) also record *A. gomezianus* for the Lakhimpur district of Assam.

ssp. *zeylanicus* Jarrett, ssp. nov.

Artocarpus lakoocha auct. non Roxb., Thwaites, Enum. Pl. Zeylan. 262. 1861; Beddome, For. Man. 219. 1873, pro parte; Trimen, Handb. Fl. Ceylon 4: 99. 1898; Cooke, Fl. Bombay 2: 657. 1907, p.p.; Bourdillon, For. Trees Travancore, 371. 1908, p.p.; Talbot, For. Fl. Bombay 2: 529. 1911, p.p., incl. fig. 533; Fischer in Gamble, Fl. Madras 3: 1369. 1928, p.p.; Macmillan, Trop. Pl. & Gard. ed. 4. 250. 1935; Abeyes. & Rosayro, Checklist Ceylon, 48. 1939; Watanabe, Ic. Econ. Pl. S. Asia 2: 527. 1945.

Artocarpus lakoocha Roxb. var. *β gomeziana* (Wall.) Trimen, Handb. Fl. Ceylon 4: 99. 1898, quoad descr. et spec. cit.

Artocarpus gomezianus Tréc., Worthington, Ceylon Trees. 420. 1959.

Differt ab typo *ramulis junioribus* saepe appresse pubescentibus, pilis undulatis, cinereis, raro flavis, *foliis* ovatis, ovati-lanceolatis, ovati-ellipticis vel elliptici-oblongis, acumine ad 2 cm. longo, basi subcordata, late rotunda vel late cuneata, costa nervis lateralibusque subtus prominentibus, venulis prominulis, pubescentibus, pilis canescens undulatis, vel glabris, nervis lateralibus utrinque 10–13, petiolo (7–)13–25(–30) mm. longo, *capitulis masculis* 8–11 mm. diametro, globosis, pedunculis 5–18 mm. longis, *syncarpiis* 3 cm. diametro, flavis, carne flava, pedunculis 13–15(–20) mm. longis.

HOLOTYPE: Madras, Wight 2717 (κ); isotypes (c, GH, L).

VERNACULAR NAMES: *otamb*, *watamba*, *lowi*, southern India; *kanagana*, Ceylon. USES: the fruit is eaten and the tree appears to be planted in both Ceylon and southern India.

DISTRIBUTION: in evergreen forests to 3000 ft.; in the wetter parts of the Western Ghats and Ceylon.

India. Cutahey, Buchanan, Mar. 1801 (BM, ♀); Malabar, Concan, Stocks & Law (GH, ♀); Kanara, Yacombi, Cooke, Feb. 1893 (κ, ♂, ♀). BOMBAY. North Kanara, Karwar, Fernandes 119 (A, ♂); Sanklu [? Sangli], Stocks (κ, ♂); Supa, Fernandes 1143 (A, BLAT, ♀), Ritchie 1381 (κ, ♂). MYSORE. Marnhalli,

Meebold 8435 (κ, ♂). COORG, Near Mercara, *Hohenacker 557* (BM, c, κ, L, ♂). MADRAS. Mangalore, *Wight 2717*, Mar. 1852 (c, GH, κ, L, ♀).

Ceylon. *Macrae 692* (BM, CGE, ♂), *Thwaites CP 2232* (BM, CGE, GH, P, ♂), *2463* (κ, ♂); Galle, *Champion* (CGE, ♀); Galle, Batapola, *Worthington 2462* (BM); w. of Ginganga, Hiniduma, *Worthington 2312* (BM, ♂); Kadugannawa, Kolugala, *Hancock 1379* (BM); Kadugannawa, Udawela Fort Jungle, *Worthington 1426* (BM, ♀); Narawella [= Nuwara Eliya], *Champion* (CGE, ♂); Ratnapoora, *Thwaites CP 2831* (BM, CGE, GH, κ, P, ♀). **Cultivated.** CEYLON. Mellue, *Gardner* (κ, ♀); Peradeniya, Hort. Bot., *Worthington 6744* (CGE, ♀), *Worthington*, Feb. 1955 (CGE, ♂).

Artocarpus gomezianus ssp. *zeylanicus*, which is described here from the Western Ghats and Ceylon, has not previously been distinguished from *A. lakoocha*. However, within the Indian subcontinent, the latter appears to be restricted, as an indigenous tree, to the north and east. The new entity is differentiated by the smaller, globose head (8–11 mm. diameter *vs.* 12–25 × 10–18 mm.) and the longer peduncle (5–18 × 1 *vs.* 2–5 × 2 mm.) of the male inflorescence, by the smooth surface of the female head at anthesis and the shorter exertion of the styles (to 0.3 mm. *vs.* 1–1.5 mm.) and, apparently, by the smaller size and smoother surface of the mature syncarp. In addition, the collections seen from India have rather distinctive ovate-lanceolate leaves, which are densely greyish pubescent beneath. In those seen from Ceylon, on the other hand, the leaves vary to elliptic-oblong in outline and these and the twigs are often subglabrous, so that specimens are not clearly distinguishable from *A. gomezianus*, *sensu stricto*. Since the dimensions of the male inflorescences, although usually smaller in the western entity, also overlap, it seems best to treat the latter as a subspecies of *A. gomezianus*. The nature of the variation found in Ceylon is not entirely clear, but it appears to occur between different trees and not merely to represent sapling and adult stages. Subglabrous collections from Ceylon were identified with *A. gomezianus* by both Thwaites and Trimen, and were described by the latter under the name *A. lakoocha* var. *β gomeziana*.

32. **Artocarpus dadah** Miq. Fl. Ind. Bat. Suppl. 420. 1861, Ann. Mus. Lugd.-Bat. 3: 213. 1867; S. Moore, Jour. Bot. 63, Suppl. 112. 1925; Corner, Gard. Bull. Singapore 10: 282. 1939, Wayside Trees, 653. 1940. Holotype, Sumatra, *Teymann HB 4391* (v); isotypes (BO, κ, L).

Artocarpus mollis Miq. Fl. Ind. Bat. Suppl. 420. 1861, non Wallich, 1831 (nomen nudum), Ann. Mus. Lugd.-Bat. 3: 211. 1867. Holotype, Sumatra, *Teymann HB 4211* (L); isotype (BO).

Artocarpus rufescens Miq. Fl. Ind. Bat. Suppl. 420. 1861; Renner, Bot. Jahrb. 39: 370. 1907. Holotype, Sumatra, *Teymann HB 3793* (v); isotypes (BO, κ, L).

Artocarpus tampang Miq. Fl. Ind. Bat. Suppl. 421. 1861, Ann. Mus. Lugd.-Bat. 3: 211. 1867. Holotype, Sumatra, *Teymann HB 3997* (v); isotypes (BO, κ, L).

- Ficus tampang* Miq. Fl. Ind. Bat. Suppl. 425. 1861. Holotype, Sumatra, *Teysmann HB 710* (U); isotype (BO).
- Ficus inconstantissima* Miq. Fl. Ind. Bat. Suppl. 431. 1861. Holotype, Sumatra, *Teysmann HB 3529* (U); isotypes (BO, CAL, L).
- Artocarpus inconstantissima* Miq. Ann. Mus. Lugd.-Bat. 3: 211. 1867.
- Artocarpus dadah* Miq. var. *pubescens* Miq. Ann. Mus. Lugd.-Bat. 3: 213. 1867. Holotype, Sumatra, *Korthals s.n.* (L).
- Artocarpus erythrocarpa* Korthals ex Miq. Ann. Mus. Lugd.-Bat. 3: 213. 1867, pro syn.
- Artocarpus lakoocha* Roxb. var. *malayana* King in Hook. f. Fl. Brit. Ind. 5: 544. 1888; King, Ann. Bot. Gard. Calcutta 2: 15, excl. spec. *De Fretes*, Amboina. Syntypes, Malaya, King 1640, 4187, 5653 (CAL, not seen; duplicates examined, K, etc.).
- Artocarpus reniformis* Becc. For. Borneo, 631. 1902. Syntypes, Sarawak, *Beccari PB 3107, 3551* (FI); lectotype, *Beccari PB 3107* (FI).
- Artocarpus peltata* Merr. Jour. Str. Br. Asiat. Soc. 85: 166. 1922. Holotype, British North Borneo, *Villamil 168* (PNH, not seen, photograph in A); isotype (BO).
- Artocarpus lakoocha* auct. non Roxb., King in Hook. f. Fl. Brit. Ind. 5: 543. 1888, pro parte; King, Ann. Bot. Gard. Calcutta 2: 14. 1889, p.p., quoad spec. *Griffith 4666*, *Maingay 1479*; Ridley, Fl. Malay Penin. 3: 355. 1924.
- Artocarpus dasyphylla* auct. non Miq., Merr. Pl. Elmer. Born. 46. 1929.

Deciduous trees, height to 35 m. Twigs 2.5–5 mm. thick, rugose, densely short-pubescent, hairs red-brown or fulvous, straight, varying undulate, a few sometimes longer and hooked at tip. Leaves 10–30 × 5–17 cm., obovate- or elliptic-oblong, varying to ovate-elliptic, acute or acuminate, base rounded, varying to broadly cuneate or shallowly cordate, margin entire; juvenile leaves with the lamina pinnatifid or reduced to a narrow sinuate wing along the midrib; main veins prominent beneath, reticulum less so; glabrous above, or nearly so, except for the short-pubescent main veins, venation beneath densely to thinly pubescent, hairs rufous to colourless, patent, straight or slightly undulate (in Borneo, except British North Borneo, hairs often inserted along edges of reticulum and appressed over areolae), subdeciduous, the lower surface scabrescent, varying persistent; lateral veins 10–20 pairs, curved; intercostals parallel; dark green, drying dark or reddish brown to blue-grey above, pale or reddish brown beneath, the areolae sometimes greyish and, with the colourless hairs, appearing glaucous, venation concolorous or often nigrescent; petiole 5–20 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: male head 8–15 mm. across, globose or pulvinate; perianths of 2 or 3 free segments 0.3 mm. long; stamen 0.5 mm. long, filament cylindric, abruptly contracted above, anther-cells globose, 0.2 mm. long; bracts stoutly stalked, heads narrowly peltate, to 0.4 mm. across, these and perianths short-ciliate; peduncle 8–15 (Borneo, 8–20) × 1 mm., indumentum as twigs; female head with peltate bracts already fallen (densely covering young head) and styles exerted to c. 0.5 mm. through low papillae. *Syncarp* to c. 5 cm. across, subglobose, green with deep pink flesh, the surface smooth, velutinous; wall c. 7 mm. thick; proximal region of perianths free, fruiting perianths sev-

eral, fleshy, "seeds" (indurated endocarps) ellipsoid, 12×8 mm.; core c. 15 mm. across; peduncle 12–25(–40) (Borneo, 23–45(–80)) \times 4 mm., indumentum as twigs.

VERNACULAR NAMES: *tampang* (Malay), Malaya, Sumatra, Borneo; *dadah*, Sumatra (recorded only twice).

DISTRIBUTION: in evergreen forest to 3000 ft.; Tenasserim, Siam, Malaya, Sumatra, Simalur, Banka, Borneo.

Lower Burma. TENASSERIM. Mergui: Mergui range, *sine nom.* 421 (DD, ♀); Thamihla Chaungbya, *Po Khant* 13252 (K). SIAM. Phetchbun, Lom Kao, Ban Phuhee, *Smitinand* 2587 (CGE). PENINSULAR SIAM. Kaw Pa-ngan, *Kerr* 1187 (BM, ♀); Ranawng, Nok Nang, *Kerr* 16835 (BM, ♀); Satul, Klawng Ton, *Kerr* 14594 (BM, ♀); Trang, Chawng, *Kerr* 15170 (BM, ♂), *Put* 2371 (CGE); Trang, Kuantan, *Kerr* 17488 (BM, ♀); P. Terutao, *Kerr* 14229 (BM, ♂).

Malaya. KEDAH. *Meh* CF 21885 (SING); Gunong Raya, *Dolman* CF 21496 (SING, ♀). PROV. WELLESLEY. Krian, *Ridley* 9385 (CAL, SING, ♀); Kubang Ulu, *Curtis*, June 1890 (SING, ♀); Tasek Gelugur, *Ridley* 6978 (BM, ♂), 6980 (SING, ♂, ♀). PERAK. *Scortechini* 37b (L), *s.n.* (BM, K, P, SING, ♂, ♀); Larut, *King* 2678 (K, L, ♀), 4187, Apr. 1883 (K, ♀); Larut, Chandraing, *King* 5653, Mar. 1884 (BM, K, L, P, ♀); Larut, Goping, *King* 6098 (BM, BO, K, P, ♀); Sungei Larut, *Wray* 2479 (SING, ♂); Trong, *Wray* 3176 (SING, ♂, ♀); Waterfall Hill, *Wray* 2560 (SING, ♀). KELANTAN. *Walton* KEP 32681 (KEP). TRENGGANU. Bukit Kajang, Ulu Bendol, Kemaman, *Corner*, Nov. 1935 (SING). PAHANG. Cameron Highlands, *Batten Pooll*, Nov. 1939–Jan. 1940 (SING); Gali near Raub, *Burkill & Haniff* SFN 16918 (SING, ♂); Kuantan, *Lamban* CF 2707 (K, SING, ♀); Sungei Rompui, *Bidin* CF 15658 (SING, ♀). SELANGOR. Klang Gates, *Murdoch* 57 (BM, ♂); Kuala Lumpur, *Mohamor*, June 1890 (SING, ♀); Kuala Lumpur, Weld Hills For. Res., *Ahmad* CF 2949, 5025 (SING, ♀), *Guard* CF 863 (SING, ♂). NEGRI SEMBILAN. Triang Res., *Tahir* CF 607 (SING, ♀). MALACCA. *Maingay* 1479 (BO, GH, K, L, ♂, ♀); Ayer Punnas, *Griffith* 4666 (K, P, ♀). JOHORE. Kluang For. Res., *Holtum* SFN 9204 (K, SING, ♂); Sungei Berassau, Mawai-Jemalaung road, *Corner*, Jan. 1936 (SING); Sungei Kayu, Mawai-Jemalaung road, *Kiah* SFN 32185 (BO). LANKAWI ISLANDS. *Wyatt-Smith* KEP 71197 (K, KEP, ♂, ♀); near Kuah, *Curtis* (SING); P. Butong, *Curtis* 906 (K, SING, ♀). PENANG. *King* 1532 (K, ♂), 1640, Aug. 1881 (BO, CGE, K, ♀), *Wallich* 4658B (CGE); Government Hill, *Curtis* 1222 (SING, ♂); West Hill, *Curtis* 1251 (SING, ♀), 1743 (CAL, SING, ♂). SINGAPORE. *Cantley* 3086 (SING, ♂); Bukit Kalang, *Ridley*, 1892 (SING); Bukit Timah, *Ngadiman* SFN 34682 (A, BO, K, P, SING, ♂), *Ridley* 4722 (BM, K, L, P, SING, ♀); Chan Chu Kang, *Ridley* (SING, ♀); Changi, *Ridley* 3358 (CAL, K, SING, ♂, ♀), 4724 (K, ♂); Government House Domain, *Best* SFN 25995 (SING, ♀); MacRitchie Reservoir, Thompson Road end, *Corner*, June 1937 (SING); Mandai road, *Corner* SFN 32545 (K, SING), *Ridley* 4130 (BM, SING, ♀); 11½ miles Mandai road, by shore of Seletar Reservoir, *Sinclair*, Mar. 1953 (K); Pulau Ubin, *Ridley* 4721 (SING, ♀); Reservoir Jungle, *Corner*, Feb. 1937 (SING, ♂).

Sumatra. *Grashoff* 1032b (BO, L, ♀), *Korthals* (L, ♀). TAPANULI. Sibide, Parduaan, *Rahmat si Boeea* 6096 (L, ♂); Padang Lawas, Purbasinamba, *bb* 6202 (BO). WEST COAST. Fort de Kock, *Teysmann* 710 (BO, U); Mt. Sago near Pajahkumbuh, *Meijer* 7197 (L); Priaman, *Diepenhorst* 2186 (P). EAST COAST. Amplas, *Jochems* 3168 (BO); Asahan, Aek Salabat, *Rahmat si Boeea* 9622 (A, L, ♂); Asahan, Huta Padang, *Krukoff* 4368 (A, BO, L, NY, SING, ♂); Asahan,

Simpang Toba, *bb* 6344, 7184 (BO, L); Beneden Langkat, Alur Gusta, *bb* 16375 (A, BO, L); Langkat, Sungei Sedapan, *bb* 9364 (BO); Lubuk Mambang, *Koorders* 10453 (BO, ♀); Sibolangit, *Lörzing* 5151 (BO, L, ♀). DJAMBI. Danau Lama, *bb* 13640 (BO, ♀). PALEMBANG. Banjuasin and Kubustreken, *NIFS T* 65 (BO, L, U, ♀), 777 (BO, K, L, SING, ♀); Banjuasin, Bajunglintjir, *NIFS T* 902 (BO, L, ♂); Batu Radja, *Teysmann HB* 3529 (BO, CAL, L, U); Dermo Enim, *Teysmann HB* 3793 (BO, K, L, U, ♂, ♀); Komering Ulu, *Grashoff* 579 (BO); Lematang Ilir, Darmo, *bb* 8720 (BO); Lematang Ilir, Gunong Megang, *NIFS T* 889 (BO, L, ♂), 1207 (BO); Lematang Ulu, *Grashoff* 179 (BO, L), *Lambach* 1200 (BO, L, ♀); Muara Dua, *Grashoff* 436 (BO, L, ♀), *Teysmann HB* 3856 (BO, P); Muara Dua, Kisau, *bb* 9234 (BO); Mulak Ulu, *Grashoff* 330 (BO, L, ♂); Pandananan, Oganulu, *Teysmann HB* 3742 (P), 3997 (BO, K, L, U); River Ruput, W. Suka Radja, *Forbes* 2948a (CAL, L); Tandjong Ning, River Bliti, *Forbes* 2789 (BM, L, SING, ♀). LAMPONGS. Kebang, *Teysmann HB* 4211 (BO, L); Mangala, *Teysmann HB* 4391 (BO, K, L, U, ♀). SIMALUR. *Achmad* 1259 (BO, K, L, P, SING, U, ♀); Landschap Tapah, Defajan, *Achmad* 1805 (BO, K, L, SING, ♀). BANKA. Blinju, *Teysmann HB* 7249 (BO, K, L, ♀), *Vordermans* 41 (BO, ♀); Djebus, *Teysmann HB* 7255 (C, K, L, P); Pangkalpinang, *Teysmann HB* 6842 (BO, K, L, ♀), 6856 (BO, C, K, L, P, ♂); Sungei Liat, *Teysmann HB* 7256 (L, P); Zapadong, *Teysmann HB* 3290 (P). BILLITON. Tandjungpandan, *Teysmann* (BO). RIOUW ARCHIP. P. Bintang, *Teysmann HB* 7285 (BO, K, L, P, ♀).

Borneo. SARAWAK. Kuching, *Beccari PB* 3107, Nov. 1867 (FI, K, ♀), 3551, June 1867 (A, FI, ♂); Nanga Temulan, *Daud & Tachun* 35690 (SING, ♀). WEST BORNEO. Sambas, Perigi Limus, *bb* 7064 (BO, ♀); Sungei Sambas, *Hallier* 1153 (BO, L, SING, ♂). SOUTH AND SOUTHEAST BORNEO. Martapura, Djungur, *bb* 10377 (BO, ♂, ♀); Tanah Bumbu, Kampong Baru, *bb* 13308 (BO, L), 13366 (BO, K, L, ♀). EAST AND NORTHEAST BORNEO. Balikpapan: *Lam* 3871 (L); Mentawir, *Sauveur* 97 (K, ♂, ♀). Berouw: Domaring, *bb* 18865 (A, BO, L, SING, ♂); Inaran, *bb* 12175 (BO). W. Kutei: Longbleh, *bb* 16133 (BO, L), 16145 (A, BO); Tandjong Isui, *Endert* 1945 (A, K, L, ♂, ♀); Upper Mahakam, Udjoh Bilang, *bb* 20612 (A, BO, L). E. Kutei: Loa Djanan, w. of Samarinda, *Kostermans* 6644 (L), 9970 (L, ♂, ♀); Tandjong Bangko region, near mouth of Mahakam River, *Kostermans* 7018 (L). BRITISH NORTH BORNEO. *Agama* 484 (A, K, ♀); Elphinstone prov., Tawao, *Elmer* 21110 (A, BM, K, L, ♀); Mt. Kinabalu, Dallas, *Clemens* 26322 (A, BM, K, L, ♂, ♀), 27444 (A, BO, BM, K, L, ♀); Sandakan, *Melegrito* 9044 (SING), *Ramos* 1904 (A, BM, K, L, ♂), *Villamil* 168, Mar. 1916 (BO, PNH, ♀); Sandakan, Ebpura, Beatrice Road, *Alendre A* 3252 (L, SING, ♀); Sandakan, Leila For. Res., Bukit Makara, *Wood SAN A* 3476 (A, K, L, SING, ♂).

This common and variable species was described under six different specific names by Miquel in 1861. Of these, the one chosen here is *Artocarpus dadah*. This has been the name most widely used on herbarium specimens and Corner, in 1939, correctly identified as *A. dadah* the Malayan entity which had hitherto been regarded as representing *A. lakoocha*. The latter is a species of the monsoon forest which has not been found south of the Siamese border, and the error arose from its treatment by King in his monograph. He described under *A. lakoocha* a variety *malayana*, citing three collections here referred to *A. dadah*, and giving *A. tampang* and *A. rufescens* of Miquel correctly as synonyms. However, under the type itself two further collections of *A. dadah* were listed and

the description was partly based on these. As a result, the variety was not recognized by later workers and all Malayan material was identified as *A. lakoocha*. The fourth collection cited by King under var. *malayana*, *De Fretes s.n.* from Ambon, is a sterile specimen which may be referable to *A. vrieseanus*.

The variation shown by *Artocarpus dadah* occurs chiefly in the length of the peduncles and in the indumentum. It has some geographical basis, but separation into geographical units is not possible, since the variation is continuous and is not parallel in the different characters. Collections seen from Borneo tend to have inflorescences with longer peduncles, as is indicated above in the description. In this area the indumentum of the leaves is also usually persistent, whereas elsewhere the leaves generally become subglabrous and slightly rough beneath. Some specimens from Sumatra and Malaya are, however, densely and persistently pubescent, and this character is often associated with a rather more prominent reticulum. A peculiarity found in material from Borneo (but apparently not in that from British North Borneo) is that hairs are inserted along the edges of the veins of the reticulum on the lower surface and appressed over the areolae. This is not to be confused with the minute tomentum developed from the epidermis of the areolae in some other species of subgenus *Pseudojaca*.

The characters distinguishing *Artocarpus dadah* from *A. fulvicortex* and *A. tomentosulus* are noted below under those species. The only other species occurring within its area with which *A. dadah* might be confused is *A. fretessii*, which extends into the eastern part of Borneo. This differs in the more prominent, straw-coloured reticulum of the leaves, in the paler indumentum, crisped on the twigs, and also in the smaller male inflorescences and the lobed syncarp. Characters distinguishing *A. dadah* from *A. vrieseanus* are given below.

33. *Artocarpus vrieseanus* Miq. Ann. Mus. Lugd.-Bat. 3: 212. 1867.

Artocarpus cumingiana auct. non Tréc., Diels, Bot. Jahrb. 67: 176. 1935.

Trees, height to 28 m. Twigs 2–4 mm. thick, pubescent to subglabrous, hairs red-brown to yellowish, \pm appressed and crisped or undulate, varying patent and straight or hooked at the tip. Leaves 7–30 \times 3–15 cm., obovate-oblong to elliptic or ovate-elliptic, varying narrowly oblong, oblong-lanceolate or elliptic, acute or with an acumen to 2.5 cm. long, base narrowly to broadly rounded or shallowly cordate, margin entire; main veins prominent beneath, reticulum not at all to markedly prominent; glabrous above except for the usually pubescent main veins, venation beneath moderately to sparsely pubescent, varying subglabrous, hairs colourless, weak and undulate or crisped, or some, rarely almost all, stouter and hooked at the tip; lateral veins 8–14 pairs, curved; intercostals parallel, varying reticulate; dark green, drying brown, grey-green or greenish, venation concolorous, varying straw-coloured; petiole 5–18 mm. long.

Inflorescences solitary in leaf-axils or the male heads sometimes borne

on short-shoots on older wood. *At anthesis*: *male head* (3-)5-15 mm. across, globose to short-obovoid; perianths of 3 or 4 segments, free or fused for half their length, 0.4-0.5 mm. long; stamen 0.75 mm. long, filament tapering above, anther-cells globose, 0.2 mm. long; bracts stoutly stalked, heads peltate, to 0.6 mm. across, these and perianths puberulent; peduncle $2-15 \times 1$ mm., velutinous, hairs usually crisped, varying subglabrous: *female head* with peltate bracts nearly all shed and styles exserted to 0.4 mm. through perforations in the surface (in var. *papillosus* through papillae). *Syncarp* to 6 cm. across, subglobose, yellow, drying orange to brown or black, the surface smooth, velutinous, often glabrescent, varying subglabrous and then clearly areolate; wall c. 2 mm. thick; proximal region of perianths fused, fruiting perianths numerous, thin-walled, "seeds" (indurated pericarps) ellipsoid, variously compressed, $11 \times 8-10$ mm.; core 10-15 mm. across; peduncle $3-35 \times 3$ mm., velutinous, hairs usually crisped, varying subglabrous.

DISTRIBUTION: in rain forest to 6000 ft.; Philippines (Mindanao), Celebes (Manado) ?, Moluccas, New Guinea, Bismarck Archipelago, Japan, Salawati, Aru Islands, Louisiade Archipelago, Solomon Islands.

This widely distributed species exhibits a range of variation in the type and abundance of the indumentum, the length of the peduncles, the shape of the leaves and the prominence of their venation which is greater than in any other member of subgenus *Pseudojaca*. Four variants can be distinguished, each with a consistent geographical distribution, and, although three of these are based primarily on vegetative characters, it seems desirable to describe them all at the varietal level, and so to bring some order into the rather chaotic variation presented by this species at first sight.

The most widely distributed of the varieties is var. *refractus*, which extends from Mindanao through New Guinea to the Louisiade Archipelago, and has fairly broad, obovate-oblong (varying to elliptic) leaves with moderately prominent venation and a variable indumentum, a relatively large male head (5-15 mm. across), and variable peduncles (3-15 mm. in the male inflorescence and (?2-)15-30 mm. in the syncarp). Specimens from a limited area in the mountains of eastern New Guinea, which have rather small, narrow leaves with a more strongly developed reticulum, are assigned here, but are discussed further under the variety. In the Solomon Islands, var. *papillosus* is distinguished primarily by the papillate surface of the female head at anthesis, but also by the often ovate-elliptic leaves. The indumentum is variable, as is the length of the peduncles (3-5 mm. in the male inflorescence and 5-35 mm. in the syncarp), and the male head is rather smaller than in var. *refractus* (3-8 mm. across).

The two other varieties recognized in *Artocarpus vrieseanus* have ranges overlapping that of var. *refractus* in New Guinea, but are distinguished by the thinly pubescent to subglabrous leaves, which are often rather thinly coriaceous and narrow in outline, and by the small male heads (4-7 mm. across). The type variety extends from northeastern New Guinea west-

ward to the Moluccas and perhaps Celebes (with one doubtfully identified collection from Bougainville). The leaves have a slender, slightly prominent reticulum, and these and the twigs are thinly pubescent or subglabrous; except in a few almost entirely glabrous specimens some of the hairs are consistently hooked at the tip (such hairs being found otherwise only in a few collections of var. *refractus*). The peduncles are rather long, measuring (4-)6-17 mm. in the male inflorescence and 15-35(-65) mm. in the syncarp. Finally, var. *subsessilis*, which is found in New Guinea, the Bismarck Archipelago and Bougainville, has glabrous leaves lacking a prominent reticulum. Only the young twigs are puberulent, with straight or crisped, but not hooked, hairs, and the inflorescences have short peduncles (2-3 mm. long in the male inflorescence and 3-7(-13) mm. in the syncarp).

The biological significance of these varieties, apart from var. *papillosus* which has presumably arisen through geographical isolation, is not clear. The three others appear to be genuinely distinct, and not merely adult or sapling forms. Whereas var. *refractus* occurs widely in New Guinea, var. *vrieseanus* and var. *subsessilis* have not yet been recorded from the southern regions, and these entities may be separated in northern New Guinea by slightly different ecological requirements, although no evidence in support of this can be gained from field notes.

The species that appears to be most closely related to *Artocarpus vrieseanus* is *A. xanthocarpus*, from the northern and central Philippine Islands, and the characters distinguishing the latter are discussed below, under that species. Some of the varieties of *A. vrieseanus* may, however, bear a strong superficial resemblance to two apparently less closely allied species, *A. dadah* and *A. fretessii*, and the variability of *A. vrieseanus* is such that only the complete fusion of the perianths in the syncarp provides an entirely satisfactory taxonomic distinction. The west Malaysian *A. dadah*, in addition to having the proximal region of the perianths free, differs in the colour of the syncarp, which is green with deep pink flesh (instead of yellow), in the straight hairs on the twigs (sometimes hooked at the tip), and in the more numerous lateral veins on the larger leaves (to 20 instead of 13(-14) pairs).

The range of *Artocarpus fretessii*, which extends from Borneo and the Philippines to the Vogelkop of New Guinea, overlaps that of *A. vrieseanus* to a considerable extent, but the syncarps of these two species, also, can usually be distinguished externally. In *A. vrieseanus* the syncarp is subglobose, with numerous seeds, but in *A. fretessii* it is distinctly lobed, each lobe usually containing one of the relatively few (up to 12) seeds. There is a further difference between the species in the interfloral bracts of the male heads: in the former rather few of these have well-developed, peltate heads, with stout stalks expanding gradually into the head, and there are numerous intermediates to the perianth segments, whereas in the latter there are many peltate bracts with slender stalks and well-defined heads, and few intermediates. These distinctions, and also the complete fusion of the perianths in the syncarp, have been confirmed for all the varieties

recognized in *A. vrieseanus*. No satisfactory vegetative characters can be found serving to distinguish this species and *A. fretessii* over the whole of their ranges, but notes are given below, under the three varieties with a range overlapping that of *A. fretessii*, that will, it is hoped, aid in the identification of sterile material.

KEY TO THE VARIETIES OF *ARTOCARPUS VRISEANUS*

1. Leaves without a prominent reticulum, glabrous; young twigs puberulent, the hairs straight or crisped; male peduncle to 3 mm., syncarp peduncle to 7(-13) mm. long. var. *subsessilis*.
1. Leaves with the reticulum slightly to markedly prominent beneath; reticulum and twigs usually pubescent, or if subglabrous, some of the hairs hooked at the tip.
 2. Leaves rather thinly coriaceous, often narrow, the reticulum slightly prominent beneath; reticulum and twigs subglabrous to thinly pubescent, except when nearly glabrous some of the hairs hooked at the tip; male peduncle (4-)6-17 mm., syncarp peduncle 15-35(-65) mm. long. var. *vrieseanus*.
 2. Leaves moderately to thickly coriaceous, the reticulum distinctly prominent beneath; reticulum and twigs pubescent, rarely subglabrous, the hairs undulate or crisped, rarely a few hooked at the tip.
 3. Female head papillate at anthesis (Solomon Islands). var. *papillosus*.
 3. Female head smooth at anthesis. var. *refractus*.

var. *refractus* (Becc.) Jarrett, stat. nov.

Artocarpus refracta Becc. For. Borneo, 630. 1902. Holotype, Aru Islands, Beccari s.n. (FI); isotypes (FI).

Twigs pubescent or rarely subglabrous, the hairs appressed and crisped, varying patent and straight or undulate, rarely a few stouter and hooked at the tip. *Leaves* obovate-oblong, varying obovate-elliptic, elliptic or oblong, sometimes narrow; main veins prominent beneath, the reticulum moderately, sometimes markedly, prominent, pubescent or rarely subglabrous, the hairs undulate or crisped, rarely a few stouter and hooked at the tip. *Inflorescences at anthesis: male head* 5-15 mm. across, peduncle 3-15 mm. long; *female head* with the surface smooth. *Syncarp*, peduncle (?2-)15-30 mm. long.

DISTRIBUTION: in primary and secondary forest from sea level to 6000 ft.; Mindanao, Moluccas, New Guinea, Salawati, Aru Islands, Louisiade Archipelago.

Philippines. MINDANAO. *Ahern* 676 (BO, ♀). Bukidnon: Mt. Katanglad, *Sulit* PNH 9951 (A, L, ♂). Davao: *De Mesa* FB 27486 (K, ♀); Todaya, *Copeland* 1244 (P, ♂); Todaya, Mt. Apo, *Elmer* 10932 (A, BM, BO, K, L, ♀). Zamboanga: San Ramon, *Hallier* 4671a (L). **Moluccas.** OBI. *Atasrip* 45 (L).

New Guinea. VOGELKOP. Manokwari: Bostuin Tafelberg, *Versteegh* BW 3830 (L, ♀). Sorong: Sausapor, *Versteegh* BW 4619 (L, ♂). **DUTCH NORTH NEW GUINEA.** Idenburg River, Bernhard Camp, *Brass & Versteegh* 14004 (A),

14021 (A, ♀); Mamberamogebiet, Pionier Bivac, *Lam* 730 (BO, K, L, U, ♂, ♀). DUTCH SOUTH NEW GUINEA. Bian River, *Branderhorst* 275 (BO, K, ♀); Sungei Aëndua, Mimika, *bb* 32900 (K, L). PAPUA. Central Division: Iawarere, *Brass* 674 (A, K, ♂); Mafulu, *Brass* 5184 (A, BO, US, ♀), 5394 (A, BO, K, US, ♀); Sogeri, *Forbes* 86 (BM, L, ♂). Northern Division: Isuarava, *Carr* 15351 (A, BM, K, L, SING, ♂), 15552 (BM, K, L, SING, ♂), 15762 (BM, K, L, SING); c. 8 km. n. of Saiho along road to Divinikoari, *Hoogland & Macdonald* 3492 (A, K, L, ♀); Tufi Subdistrict, halfway between Wanigela and Itoto, *Hoogland* 4822 (A, BM, K, L, ♂, ♀). Western Division: lower Fly River, e. bank, opposite Sturt Island, *Brass* 8117 (A, L, ♂, ♀). MANDATED TERRITORY OF NEW GUINEA. Madang District: Kani-gebirge, *Schlechter* 17065 (A, K, L, ♂, ♀). Morobe District: Matap, *Clemens* 11174 (A, ♀); Ogeramnang, *Clemens* 4550, 5138 (A, ♂, ♀); Quembung mission trail to Sattelberg, *Clemens* 1244 (A, ♀); Sattelberg, *Clemens* 7584 (A). SALAWATI. Kaloal, *Koster BW* 4253 (L). ARU ISLANDS. Giabulengan, *Beccari*, May 1873 (FI, ♂, ♀). LOUISIADE ARCHIP. Rossel Island, Jinju, *Brass* 28569 (A, L, ♂).

With the type of *Artocarpus refractus*, which came from the Aru Islands, Beccari cited an additional specimen, *PB* 74, from Kapaor, Papua Onin, but this is apparently not in the Herbarium Universitatis Florentinae and has not been found elsewhere.

Quite a wide range of variation is found within this variety, particularly, as noted above, in some collections from the mountains of eastern New Guinea. Elsewhere in New Guinea, var. *refractus* has not been seen from above 3000 feet (although one of the collections from Mindanao was made at 5500 feet), but from the Central and Northern Divisions of Papua, and the Madang and Morobe Districts of northeast New Guinea several collections from an altitude of 3000 to 6000 feet have been seen. Some of these (*Brass* 5184, 5394, *Forbes* 86, *Carr* 15351, 15552, 15762 and *Clemens* 11174) have rather small, narrow leaves characterized by a very strongly developed, netted reticulum and could, perhaps, be regarded as representing a distinct entity. However, the remaining four (*Schlechter* 17065 and *Clemens* 4550, 5138 and 7584) are intermediate to the typical form, having rather broadly elliptic leaves with a netted, but less prominent, reticulum.

It is not possible to give satisfactory characters for distinguishing male or sterile collections of *Artocarpus vrieseanus* var. *refractus* from *A. fretessii*, apart from the difference in the bracts mentioned above. However, in the former the male heads are usually somewhat larger, with shorter peduncles relative to the size of the head; they are also only rarely borne on short-shoots, whereas this is very common in the latter. On the whole, *A. fretessii* tends to have a smaller leaf, with a more distinct, often straw-coloured reticulum, and somewhat more ascending lateral veins, but rather similar leaves are found in the mountain form of var. *refractus*. In the eastern Moluccas and New Guinea, *A. fretessii* is also distinguished by the rather markedly cordate base of the leaf.

var. *papillosus* Jarrett, var. nov.

Ramuli juniores pubescentes, pilis appressis crispatisque, vel patentibus et rectis undulatisve. *Folia* ovati-elliptica, elliptica vel obovati-elliptica;

costa nervi lateralesque subtus prominentes, venulae prominulae, pubescentes, pilis plus minusve undulatis, ad subglabri. *Inflorescentiae ad anthesin: capitula mascula* 3–8 mm. diametro, pedunculis 3–5 mm. longis; *capitula feminea* superficie plana. *Syncarpia* pedunculis 5–35 mm. longis.

HOLOTYPE: Solomon Islands, *Kajewski* 2360 (A); isotypes (BM, K, L, P).

DISTRIBUTION: in rain forest from sea level to 4000 ft.; Solomon Islands.

Solomon Islands. BOUGAINVILLE. Kugumaru, Buin, *Kajewski* 1920 (A, K, ♂). GUADALCANAL. Berande, *Kajewski* 2436 (A, BM, K, P, ♀); Vulolo, Tutuve Mt., *Kajewski* 2501 (A, BM, P, ♀). MALAITA. Quoimonapu, *Kajewski* 2360, Dec. 1930 (A, BM, K, L, P, ♂, ♀). SAN CRISTOBAL. Balego-nagonago, *Brass* 2826 (A, K, L, ♂, ♀).

Seed formation in this variety is often somewhat irregular, so that the syncarp is slightly lobed, while the surface between the lobes remains papillate as in *A. fretessii*; the lobes, however, differ from those found in the latter species in being shallow and ill defined.

var. *vrieseanus*

Artocarpus vrieseana Miq. Ann. Mus. Lugd.-Bat. 3: 212. 1867; Renner, Bot.

Jahrb. 39: 369. 1907. Syntypes, Batjan, *De Vriese s.n.*, Celebes, Manado, *De Vriese s.n.* (L); lectotype, Batjan, *De Vriese s.n.* (L).

Artocarpus antiarifolia Becc. For. Borneo, 630. 1902. Holotype, Jobi [Japen], *Beccari s.n.* (FI); isotype (FI).

Artocarpus cumingiana Tréc. var. *stenophylla* Diels, Bot. Jahrb. 67: 177. 1935.

Holotype, northeast New Guinea, *Ledermann* 12863 (B); isotype (K).

Twigs thinly pubescent to subglabrous, except when nearly glabrous some hairs patent or recurved and hooked at tip, the rest patent to crisped. *Leaves* oblong-elliptic to elliptic or obovate-elliptic, often narrowly so; main veins prominent beneath, reticulum slightly so, indumentum as on twigs. *Inflorescences at anthesis: male head* 4–7 mm. across, peduncle (4–)6–17 mm. long; *female head* with the surface smooth. *Syncarp*, peduncle 15–35(–65) mm. long.

DISTRIBUTION: in primary and secondary forest from sea level to 3000 ft.; Celebes (Manado) ?, Moluccas (Batjan), New Guinea.

Celebes. (?) NORTH PENINSULA. Manado, *De Vriese* (L, ♀). Moluccas. BATJAN. *De Vriese* (L, ♂, ♀).

New Guinea. DUTCH NORTH NEW GUINEA. Geelvink Bay, Nabire, *Kanehira & Hatusima* 11538 (A, BO, ♂), 11584 (A, BO, ♀); Sarmi, Tor River, Dirdjan, *Leden BW* 5364 (L, ♂, ♀). MANDATED TERRITORY OF NEW GUINEA. Madang District: near the Gogol River, near Mawan village, *Hoogland* 4928 (A, K, L, ♂, ♀); Kani-gebirge, *Schlechter* 17854 (A, K, L, ♂); Wobbe, *Schlechter* 16439 (A, K, L, ♂). Sepik District: Kaiserin Augusta [Sepik] River, Felsspitze, *Ledermann* 12863, Aug. 1913 (BM, K, ♂). JAPEN. Ansus, *Beccari s.n.*, Apr. 1875 (FI, ♂); near Serui, Kaunda, *Aet & Idjan* 568 (L, ♂); Serui, Watibu, *bb* 30249 (BO, L, SING, ♀).

The type material of *Artocarpus vrieseanus* in the Rijksherbarium,

Leiden, consists of six sheets purporting to come from both Celebes and Batjan, but comparison of these indicates that only three gatherings are involved and that there has been some confusion in the labelling. The two sheets labelled as coming from Celebes, one of which has an attached submature syncarp (peduncle 55 mm.), match exactly the leaves and detached syncarp (peduncle also 55 mm.) of one of the sheets stated to be from Batjan. Since the other two gatherings are both labelled as from Batjan the record from Celebes appears somewhat doubtful at present. The second gathering consists of two sheets with immature male inflorescences attached and in an envelope (the head to 7 mm. across and the peduncle to 17 mm. long). A twig on one of these sheets, which bears a leaf and a syncarp comparing closely with the first gathering, was probably mounted here by mistake, and the other sheet is therefore chosen as the lectotype. The third gathering, which is very similar to the first, is represented by a sterile sheet from Batjan (matched by another sheet from Hasskarl's herbarium not annotated by Miquel). All the material is undoubtedly referable to the entity under consideration, since the perianths in the syncarp are completely fused, the bracts in the male head are stoutly stalked, and the leaves are thinly coriaceous with a slightly prominent reticulum. No hooked hairs were found on the leaves or twigs, but this is true of a few other almost completely glabrous collections of var. *vriseanus*, such as *Kanehira & Hatusima 11584*, which is a good match for the first gathering mentioned above.

A collection from Kugumaru, Buin, Bougainville, *Kajewski 1940* (A, BM, K, L, P, SING, ♂, ♀), may be referable to this variety; the leaves are rather broadly elliptic, and these and the twigs are definitely pubescent, but many of the hairs are hooked at the tip and the young syncarps are smooth, not papillate as in var. *papillosus*. A sterile collection from Ambon, *De Fretes s.n.* (CAL, GH, L, U), which likewise has pubescent leaves but abundant hooked hairs, may also be referable here since the leaves are, in addition, scarcely cordate (see below); it is, however, discussed further under *A. fretessii*. The latter may be distinguished vegetatively by the definitely pubescent leaves with a more prominent reticulum, the absence of hooked hairs (occasionally a few present in specimens from the Vogelkop), and, in the eastern Moluccas and New Guinea, by the rather markedly cordate leaf base.

var. *subsessilis* Jarrett, var. nov.

Ramuli juniores, puberulentes, pilis appressis et rectis crispatisve, mox glabrescentes. *Folia* elliptica vel obovati-elliptica, saepe angusta; costa nervi lateralesque tantum subtus prominentes et puberulentes vel glabri. *Inflorescentiae ad anthesin: capitula mascula* 5–7 mm. diametro, pedunculis 2–3 mm. longis; *capitula feminea* superficiei plana. *Syncarpia* pedunculis 3–7 mm. (*Floyd 3453* ad 13 mm.) longis.

HOLOTYPE: northeast New Guinea, *Hoogland 4999* (A); isotypes (K, L).

DISTRIBUTION: in primary and secondary forest from sea level to 5500 ft.; New Guinea, Bismarck Archipelago, Solomon Islands (Bougainville).

New Guinea. VOGELKOP. Steenkool, road to Tembuni, *van Royen* 3591 (L). DUTCH NORTH NEW GUINEA. Hollandia, Holtekang, *Brouwer* BW 1539 (L, ♀); Wissel Lake region, Lake Tigi, *Eyma* 4883 (L, ♀); Wissel Lake region, foot of Mt. Bubi-ro and Enarotali, *Eyma* 5124 (L, ♀). PAPUA. Milne Bay District: Cape Vogel Peninsula, Menapi, *Brass* 21660 (A, ♀). Northern Division: Kokoda, *Carr* 16420 (L); Tufi Subdistrict, near Koreaf village, *Hoogland* 4813 (A, BM, K, L, ♀). MANDATED TERRITORY OF NEW GUINEA. Madang District: Gogol River valley, near Jal village, *Hoogland* 4999, July 1955 (A, K, L, ♂, ♀). Morobe District: Lae, Botanic Gardens ("indigenous"), *Womersley* NGF 9079 (A, L, ♀). NEW BRITAIN. Keravat, *Floyd* 3453 (A, BM, K, L, ♀). **Solomon Islands.** BOUGAINVILLE. Teop Island *Waterhouse* 46 (K, ♂).

This variety can readily be distinguished from *Artocarpus fretessii* by the almost entirely glabrous leaves lacking a prominent reticulum.

34. *Artocarpus xanthocarpus* Merr. Publ. Gov. Lab. Manila 17: 10. 1904, "*xanthocarpa*," Philip. Jour. Sci. 1, Suppl. 43. 1906; Elmer, Leaf. Philip. Bot. 2: 626. 1909. Holotype, Luzon, *Whitford* 367 (PNH, destroyed); isotypes (K, P, US); lectotype (P).

Artocarpus lamellosa Blanco, nomen dubium, Elm. Leaf. Philip. Bot. 2: 625. 1909.

Artocarpus lanceolata auct. non Tréc., Merr. Enum. Philip. Pl. 2: 42. 1923.

Artocarpus rubrovenius auct. non Warb., Merr. Philip. Jour. Sci. Bot. 3: 401. 1908.

Small trees, height to 8 m. *Twigs* 1.5–3 mm. thick, smooth or finely rugose, appressed-puberulent, soon glabrescent. *Leaves* 5.5–20 × 2.5–9 cm., obovate-elliptic, varying obovate- or elliptic-oblong, with an acumen to 3 cm. long, base cuneate, varying narrowly rounded, glabrous, margin entire; main veins prominent beneath, intercostals slightly so; lateral veins 6–11 pairs, curved; intercostals few, not parallel; green, drying brownish or greenish, venation straw-coloured, reddish or nigrescent in young leaves; petiole 5–23 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: male head 3–6 × 3–4 mm., globose to obovoid; perianths tubular, bilobed above, 0.5 mm. long; stamen 1 mm. long, filament cylindric, tapering above, anther-cells ellipsoid, 0.2 mm. long; bracts slenderly stalked, heads peltate, to 0.3 mm. across, these and perianths ciliate; peduncle 2–3 × 0.5 mm., velutinous; female head with peltate bracts mostly shed and styles exerted to 0.8–1 mm. through low papillae. *Syncarp* to 5 cm. across, subglobose, shallowly lobed, yellow, drying pale or reddish brown, the surface smooth or nearly so, velutinous, with a few persistent bracts; wall c. 3 mm. thick; proximal region of perianths fused, fruiting perianths several, thin-walled, "seeds" (pericarps with an indurated endocarp) ellipsoid, 8 × 6 mm.; core c. 4 mm. across; peduncle 6–11 × 3 mm., velutinous.

DISTRIBUTION: in forest to 1300 ft.; Mangsi Islands, northern and central Philippine Islands.

Borneo. MANGSI ISLANDS. *Wilkes* (GH, ♂, ♀). Philippine Islands. MINDORO.

Merritt FB 9894 (BO, US, ♂); Mansalay, Mt. Yagaw, Conklin PNH 17465 (A, L, PNH, ♂). BATANES ISLANDS. Fenix BS 3581 (BO, ♂), 3814 (NY, US, ♀); Mt. Iraya, Ramos BS 80012 (K, NY, ♂, ♀), 80305 (K, NY, ♀). LUZON. Benguet: Leano FB 24715 (NY, US, ♀). Cagayan: Klemme FB 6670 (K, NY, US, ♂). Bataan: Lamao River, Borden 183 (A, NY, ♂); Lamao River, Mt. Mariveles, Whitford 367, June 1904 (K, P, US, ♀). Laguna: Majayjay, Curran & Merritt FB 8055 (NY, P, US, ♂). Tayabas: Labitag FB 25414 (A, K, P, US, ♂, ♀). Camarines: Aguilar FB 14345 (US, ♂); Camarines Sur, Iriga, Vidal 1539 (A, K, ♂); Mt. Bagacay, Ramos & Edano BS 33925 (SING, ♀). Sorsogon: Irosin, Mt. Bulusan, Elmer 16247 (BM, GH, K, L, ♂). BOHOL. Ramos 42581 (BM, BO, P, SING, ♀). SIKUIJOR ISLAND. Piper 398 (K, P, ♀).

Artocarpus xanthocarpus is, as noted above, apparently most closely allied to *A. vrieseanus*, from which it differs in the longer styles, exerted to c. 1 mm. at anthesis instead of only 0.4 mm., and the slenderly stalked bracts in the male head. Otherwise it is rather similar to *A. vrieseanus* var. *subsessilis*, but it may be distinguished by the base of the leaf, which is usually cuneate and slightly decurrent, instead of rounded or auriculate. The small, entirely glabrous leaves, lacking a prominent reticulum, give *A. xanthocarpus* a strong superficial resemblance to *A. nitidus* ssp. *nitidus*, which also occurs in the Philippines, and distinguishing characters are given below, under the latter entity.

The type material of *A. xanthocarpus* bears mature syncarps only, but styles 1 mm. long have been found persisting on the specimen at the Muséum National d'Histoire Naturelle, Paris. The Wilkes expedition collection from the Mangsi Islands off the northeastern tip of Borneo represents, at present, a rather outlying locality for the species. However, although the specimen is in rather poor condition, it, too, has the long styles on the syncarp and the characteristic, very small male inflorescences. The collections from the Batanes Islands are all distinguished by having a very long, slender acumen to the leaf.

35. *Artocarpus fretessii* Teysm. & Binnend. in Hassk. Abh. Naturf. Ges. Halle 9: 189. 1866, "*Fretissi*"; Merr. Interpr. Rumph. Herb. Amb. 191. 1917.

Metrosideros spuria Rumph. Herb. Amb. 3: 26. t. 13. 1743.

Antiaris fretessii Teysm. & Binnend. Cat. Hort. Bog. 84. 1866, nomen nudum.

Artocarpus dasyphylla Miq. Ann. Mus. Lugd.-Bat. 3: 212. 1867; Renner, Bot. Jahrb. 39: 369. 1907; J. J. Smith, Ic. Bogor. 3: 83. 1907. Syntypes, Celebes, Riedel HB 5841, Teysmann HB 5787 (v); lectotype, Teysmann HB 5787 (v).

Artocarpus erythrocarpa Teysm. ex Miq. Ann. Mus. Lugd.-Bat. 3: 212. 1867, pro. syn.

Prainea rumphiana Becc. For. Borneo, 636. 1902.

Artocarpus dasyphylla Miq. var. *flava* J. J. Smith, Ic. Bogor. 3: 85. t. 234. 1907.

Artocarpus leytenensis Elm. Leaf. Philip. Bot. 1: 279. 1908, 2: 622. 1909; Merr. Enum. Philip. Pl. 2: 42. 1923. Holotype, Leyte, Elmer 7243 (PNH, destroyed); isotypes (A, BO, K); lectotype (K).

Artocarpus paloensis Elm. Leaf. Philip. Bot. 1: 280. 1908, 2: 621. 1909. Holotype, Leyte, *Elmer 7244* (PNH, destroyed); isotypes (A, BO, K); lectotype (K).

Artocarpus rotundifolia Elm. ex Merr. Enum. Philip. Pl. 2: 42. 1923, pro syn.

Trees, height to 40 m., buttresses small or none, bark pale brown, peeling off in flakes. *Twigs* 1.5–4 mm. thick, pubescent, hairs pale yellow to rufous, usually subappressed and crisped. *Leaves* 6–29 × 3–12 (–32 × 16) cm., obovate-oblong to elliptic, acute, attenuate or acuminate, base broadly cuneate to shallowly cordate (varying to deeply so in the Moluccas and New Guinea), margin entire; juvenile leaves pinnatifid; main veins and reticulum distinctly prominent beneath; glabrous above or nearly so except for the pubescent main veins, venation beneath moderately to sparsely pubescent, hairs colourless, straight or slightly undulate; lateral veins 9–13 pairs, curved, basal 2–4 pairs crowded; intercostals parallel; dark green above, pale green or greyish beneath, usually drying greyish or brownish, paler beneath, venation concolorous, varying straw-coloured; petiole 5–15 mm. long.

Inflorescences solitary or paired in leaf-axils, or more frequently on short-shoots on older wood. *At anthesis: male head* 3–7 mm. across, subglobose or obovoid; perianths of 2 or 3 free segments 0.4–0.5 mm. long; stamen 0.8 mm. long, filament slightly flattened, tapering above, anther-cells subglobose, 0.15 mm. long; bracts slenderly stalked, heads peltate, to 0.3 mm. across, these and perianths sparsely ciliate; peduncle 3–7 mm. long, short-pubescent; *female head* with peltate bracts mostly shed and styles exerted to 0.5 mm. through papillae. *Syncarp* to 4 cm. across, with one to several subglobose lobes, yellow, or dark red to purple, drying olive-brown to rufous, the surface smooth over the lobes, papillate between them, short-pubescent, with a few persistent bracts; wall c. 2 mm. thick over lobes; proximal region of perianths free, fruiting perianths 1–c. 12 (New Guinea, 1 or 2), thin-walled, “seeds” (thin, horny pericarps) subglobose, 8 × 7 mm.; core c. 4 mm. across; peduncle 20–25 (–30) mm., short-pubescent.

VERNACULAR NAMES: *maumbi*, *kelembi*, Celebes; *taewan*, Ambon.

DISTRIBUTION: in forest up to 2000 ft.; eastern Borneo, Philippines, Celebes, Moluccas, New Guinea (Vogelkop).

Borneo. SOUTH AND SOUTHEAST BORNEO. Martapura, Tewingan, *Boschbouwprefstation 2108* (BO, ♂); Martapura, Twang Bangkal, *bb 2475* (BO, L, ♀). EAST AND NORTHEAST BORNEO. Loa Haur, w. of Samarinda, *Kostermans 6902* (L, ♂, ♀). BRITISH NORTH BORNEO. Kamang-sian, *Goklin 1302* (K, ♂).

Philippine Islands. PALAWAN. Brooks Point, Addison Peak, *Elmer 12609* (A, BM, K, L, ♂, ♀); Puerto Princesa, Mt. Pulgar, *Elmer 12944* (A, BM, K, L, ♀). LEYTE. *Franco FB 26409* (P), *Wenzel 811* (BM, GH, ♀); Abuyog, Lake Danao, *Krukeberg*, Sept. 1945 (A, ♂); Palo, *Elmer 7243*, Jan. 1906 (A, BO, K, ♀), *7244*, Jan. 1906 (A, BO, K, ♂, ♀). BILIRAN. *McGregor BS 18663* (A, BO, P, SING, ♀). PANAY. Ilo-ilo: Miagao, *Vidal 3833* (A, K, ♂, ♀). MINDANAO. Surigao: *Ramos & Pascasio BS 34350* (BM, L, NY, SING, ♀). CAMIGUIN DE MINDANAO. *Ramos 1196* (BM, P, U, US, ♀).

Celebes. NORTH PENINSULA. Gorontalo: Molinggapoto, *bb* 18022 (A, BO, L). Minahassa: Manado, *Koorders* 19061 (BO, L), *Riedel HB* 5841 (BO, L, U, ♀), 7264 (BO, P), *Teysmann HB* 5723 (BO), 5863 (BO, L, U); Sondaho, *bb* 5573 (BO, L); Tana Wangko, *Teysmann HB* 5787 (BO, U, ♀); Kajuwatu, *Koorders* 19039, 19048, 19055 (BO, L), 19058 (BO, L, ♀), 19431 (BO); Lubu, Amurang, *Koorders* 19052 (BO, L, ♂); Masuka, *Koorders* 19185 (BO, L); Pakuere, *Koorders* 19045 (BO, L); Pinamorangan Mts., *Koorders* 19054 (BO, K, L, ♀); Ratahan, *Koorders* 19043 (BO), 19060 (BO, L, ♀), 19306 (BO); Sembolei, *Koorders* 19062 (BO, ♀); Tondano, *Koorders* 19312 (BO, ♀). CENTRAL CELEBES. Malili, *NIFS Cel./V-216 no. 226* (BO, L); Malili, Toli Toli, *NIFS Cel./V-216 no. 109* (BO, ♂); Malili, Usu, *NIFS Cel./III-55 no. 81* (BO, ♀), *no. 238* (BO, L, ♂); Palu, Tomado, *bb* 28212 (BO, L); Poso, Tokosondo, *bb* 17977 (A, BO). SOUTHWEST PENINSULA. Baleh-Angien, *Teysmann HB* 12359 (BO, L, ♀), 12481 (BO); Bonthain, Saluang, *NIFS Cel./I-19* (BO, L, ♀); Maleku, *bb* 23909 (BO, L). SOUTHEAST PENINSULA. Kolaka, Parso, *bb* 32510 (A, BO, L, ♀). P. MUNA. Labunti, *bb* 6041 (BO, L, U, ♀).

Moluccas. TALAUD ISLANDS. Karakelang, e. of Beo, *Lam* 2626 (L, ♀). HALMAHEIRA. Djailolo, Tugair, *bb* 23734 (A, BO, L); Galela, *Beguín* 1867 (BO, L, ♂, ♀); W. Tobelo, *Beguín* 2303 (BO, K, L, SING, ♀). BATJAN. Nanggapil, *sine nom.* IX (BO, ♂). SULA ISLANDS. Mangoli, *bb* 29771 (A, BO, L); Sanana, Kali Waj Gaj, *bb* 28811 (A, BO, L, SING, ♂); Taliabu, n. of Samuja, *bb* 29937 (A, BO, L, SING, ♂). BURU. Wae Ula, *bb* 22801 (BO, ♂).

New Guinea. VOGELKOP. Manokwari: Momi, *bb* 33417 (A, BO, K, L, ♂); Oransbari, *Brouwer BW* 2512, 2576, 2594, *Mangold BW* 2133 (L); Prafi, *Schram* 554 (L); Ransiki, Mioswaas, *Koster BW* 1270 (L); Ransiki, Warsuwi, *Kostermans* 87 (BO, K, L, SING, ♀); Sidai, 65 km. w. of Manokwari, *Koster BW* 4450 (L, ♂); Warnapi, *bb* 33627, 33629 (BO, K, L). Sorong: Warsamson, 25 km. e. of Sorong, *Schram BW* 5904 (L).

Cultivated. MALAYA. Singapore, Hort. Bot., *Cantley* 136 (K, ♂, ♀), *Ridley* 3359 (BM, CAL, K, SING, ♂, ♀). JAVA. Bogor: Hort. Bot., VII G 105 (BO, L, ♀), VIII B 5 (L, ♂), *Sutrisno* 82 (cult. sub. VII G 105; origin Celebes), Oct. 1957 (L, ♂); Tjiliwung river, *Kostermans*, Aug. 1953 (K, L).

The nomenclatural type of *Artocarpus fretessii* is *Metrosideros spuria* [i] *Taewan mas* of Rumphius, for which Hasskarl provided an identification in 1866 in his key to the "Herbarium Amboinense" with the phrase "*Artocarpus Fretissi* T. & B. Teysm. in litt." The identity of Rumphius' *Taewan mas* with the species under consideration can be established with certainty from the plate (*t. 13A*), which shows the characteristic mature syncarps with rounded lobes and between these the papillate unexpanded surface. The artist has added a "calyx" to one of the fruits, but the likeness is unmistakable and extends to the vegetative characters, while the description is also in agreement. Hasskarl offered no identification for the second plant, *Taewan femina*, treated by Rumphius under *Metrosideros spuria*, but, from the plate (*t. 13B*), it appears to represent the same species at anthesis, when the female heads are globose with the entire surface papillate. In 1754, Linnaeus, in his key to Rumphius (Herb. Amb. 11 [resp. O. Stickman]), had incorrectly identified *Metrosideros spuria* as *Ochna jabotapita* L. (see Sprague, Proc. Linn. Soc. 165: 151-156. 1955, for a discussion of Linnaeus' later treatment of this species). Merrill, in

his consideration of the "Herbarium Amboinense" (1917), mentioned Teysmann and Binnendijk's name, but was unable to refer Rumphius' plant to any known species of *Artocarpus*. However, on the Bogor sheet of *Beguin 1876*, which was collected in 1921 in Halmaheira, there is a note to the effect that Beguin thought he had found *Metrosideros spuria*.

Artocarpus fretessii antedates by one year and must replace the name *A. dasyphylla* Miq. (1867) under which the species has been known in Indonesia. Teysmann and Binnendijk's epithet was based on the name of De Fretes, a resident of Ambon who presumably sent them the living material that appeared in their catalogue (1866) of the Hortus Bogoriensis under a *nomen nudum*, *Antiaris fretessii*, with the source given as Ambon and the vernacular name as *taewan*. The assumption that this plant was identified with *Taewan mas* and the generic name corrected to *Artocarpus* in Teysmann's communication to Hasskarl is supported by a specimen at Leiden from the Hortus Bogoriensis, collected from a plant numbered *VII G 105*, which is referable to this species and bears the determination "*Artocarpus fretessii*," with another note referring to *Antiaris fretessii* of the catalogue.⁴ (A recent collection from this tree, however, gives the source as Celebes.) There is also in existence a sterile collection by De Fretes from Amboina, *HB 5562*, which bears on the sheet in the herbarium at Utrecht a reference to *Metrosideros spuria*. However, as already noted under *Artocarpus vrieseanus*, the identity of the collection is doubtful and it is perhaps better referred to that species. It was determined only as *Artocarpus* but was cited as *A. lakoocha* by Miquel (Ann. Mus. Lugd.-Bat. 3: 313. 1867) and under *A. lakoocha* var. *malayana* (= *A. dadah*) by King (Ann. Bot. Gard. Calcutta 2: 15. 1889).

Artocarpus fretessii again shows considerable variability in both inflorescences and vegetative characters, particularly in the colour of the syncarp. Red or purple fruits are reported from Celebes and the Sula Islands, while yellow ones are recorded from Borneo, Celebes and the Moluccas. Although it would seem, from the frequent absence of syncarps from collections for which their colour is reported, that the yellow male inflorescences may be mistaken for them in the field, the variation is undoubtedly genuine. *Artocarpus dasyphylla* was described by Miquel as having red fruits, and J. J. Smith (1907) described the yellow-fruited form as var. *flava* from a plant of unknown provenance in the Hortus Bogoriensis. There appears to be no other difference correlated with that of the fruit colour, nor is there any geographical separation of the two forms. If the two were to be maintained as distinct, a new name would be required for the red form, since in Rumphius' description the fruit was stated to be yellow. There does not, however, seem to be any real justification for erecting a new variety for such a colour variant.

Variation in leaf shape, on the other hand, shows a definite pattern of distribution in which the leaf tends to become markedly cordate (and often

⁴ It seems best to take *fretessii* as the form in which Teysmann and Binnendijk intended to Latinize the name and to treat the spelling found in Hasskarl as an orthographic error.

somewhat elongate) in the Moluccas and New Guinea, and this is accompanied by a reduction in the number of lobes on the syncarp (each of which usually contains a single seed).

The distinctions between *Artocarpus fretessii* and *A. vrieseanus* are discussed fully above, under the latter species. In the Philippines *A. fretessii* overlaps the ranges of two further species with pubescent leaves. The first of these, *A. ovatus*, may be distinguished by the relatively longer and narrower leaves with more numerous lateral veins (11–20 *vs.* 9–13 pairs), and by the patent hairs on the twigs. The second, *A. subrotundifolius*, may be differentiated from all these species by the broad leaves with long petioles (25–35 mm. *vs.* 5–18 mm.).

36. **Artocarpus reticulatus** Miq. Ann. Mus. Lugd.-Bat. 3: 213. 1867, "*reticulata*," non Heyne ex Wallich, 1831 (nomen nudum), nec Hunter ex Ridley, 1909; Renner, Bot. Jahrb. 39: 369. 1907; Koord. Suppl. Fl. N. O. Celebes 2: t. 3, 3: 1. 1922. Syntypes, Celebes, *Teysmann HB 5272* (v), Ternate, *De Vriese & Teysmann s.n.* (L); lectotype, *Teysmann HB 5272* (v).

Trees, height to 30 m., with small buttresses, bark rough, grey. *Twigs* 3–6 mm. thick, rugose, puberulent with hooked hairs, or glabrous. *Leaves* 15–35 × 8–16 cm., oblong-elliptic, acute or acuminate, base rounded or broadly cuneate, margin entire; main veins and reticulum prominent beneath, the reticulum rather acutely so; glabrous, or the main veins above and the venation beneath scabrid-puberulent, the hairs hooked at the tip; lateral veins 12–15 pairs, curved, basal pairs slightly crowded; intercostals parallel; green, paler beneath, drying brown to yellow-green, usually paler beneath, venation concolorous; petiole 13–25 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* (immature) c. 15 mm. across, obovoid; perianths of 3 or 4 free segments 0.2 mm. long; stamen . . . ; bracts slenderly stalked, heads peltate, to 0.3 mm. across, short-ciliate; peduncle 13 × 1 mm., short-pubescent; *female head* with peltate bracts mostly shed and styles exerted to 1.5 mm. through prominent papillae. *Syncarp* to 6 cm. across, subglobose or lobed, orange, drying brown, the surface verrucose throughout from conical papillae, or becoming nearly smooth over the lobes, pubescent, with scattered persistent bracts; wall c. 5 mm. thick over lobes; proximal region of perianths free, fruiting perianths several, somewhat fleshy, "seeds" (indurated endocarps) ellipsoid, 12 × 8 mm.; core c. 15 mm. across; peduncle 25–45 × 4 mm., velutinous.

VERNACULAR NAMES: *maumbi*, *maumbi sela*, Celebes.

DISTRIBUTION: in forest to 2000 ft.; Celebes, Moluccas (Ternate).

Celebes. NORTH PENINSULA. Minahassa: Karaa, near Papo, *Koorders 19051* (BO, L, ♂); Lolombulan, near Pakuere, *Koorders 19049* (BO, L); Amurang, *sine nom. et num.* (BO, ♀); Amurang, Lobah Kolai, *bb 17125* (A, BO); Lemo, *bb 7536* (BO); Ratahan, *Koorders 19053* (BO, L), *Teysmann HB 5272* (BO, CAL, L,

u, ♀); Pingsan, near Kajuwatu, *Koorders* 19046, 19047 (BO, L). CENTRAL CELEBES. Malili, Kawata, *NIFS Cel./V-88* (BO, K, L, ♂, ♀). P. MUNA. Lam-iko, *bb* 21754 (A, BO, L, ♀). **Moluccas.** TERNATE. *De Vriese & Teysmann* (L).

The inflorescence characters of *Artocarpus reticulatus* are intermediate between those of *A. fretessii* and *A. subrotundifolius*, but provide clear distinctions from each of these species. The syncarp is usually strongly lobed as in *A. fretessii*, but the surface is more prominently papillate, and the styles are long-exserted as in *A. subrotundifolius* (to 1.5 mm. instead of to 0.5 mm.), though fewer seeds are formed than in the latter species. The male inflorescence, although it has been seen only when immature, apparently lies between the two other species in both the size of the head and the length of the peduncle. Vegetatively, *A. reticulatus* may be distinguished from *A. fretessii* by the glabrous or nearly glabrous leaves and twigs, and by the rather acutely prominent reticulum. From *A. vrieseanus* var. *vrieseanus* it is less readily distinguished, but the leaves are usually larger with more numerous, parallel intercostals, and a longer petiole (13–25 vs. 5–15 mm.).

37. *Artocarpus subrotundifolius* Elmer, *Leafl. Philip. Bot.* 1: 281. 1908, "*subrotundifolia*," 2: 619. 1909; Merr. *Enum. Philip. Pl.* 2: 43. 1923. Holotype, Leyte, *Elmer* 7265 (PNH, destroyed); isotypes (A, BO, K); lectotype (K).

Artocarpus nitidus auct. non Tréc., Ahern, *Timber Tree Sp. Philip.* 35. 1901, *tabula sola*.

Trees, height to 25 m. *Twigs* 4–6 mm. thick, smooth or rugose, red-brown to fulvous pubescent, hairs straight or undulate, subappressed or patent, slowly glabrescent. *Leaves* 18–36 × 11–22 cm., broadly elliptic to obovate-oblong, short-acuminate, base cordate, varying broadly rounded and slightly oblique, margin entire; main veins and reticulum prominent beneath; glabrous or nearly so above except for the pubescent main veins, venation beneath pubescent, hairs colourless, straight, or some on the main veins stout and hooked at the tip, old leaves glabrescent, slightly scabrid; lateral veins 10–14 pairs, basal 2–3 pairs crowded; intercostals parallel; bright green above, duller beneath, drying red-brown to blue-grey above, paler beneath, venation usually concolorous; petiole (15–)25–35(–65) mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* (20–)25–50 × 20–35 mm., obovoid, ellipsoid or subglobose; perianths of 3 or 4 free segments 0.6 mm. long; stamen 1 mm. long, filament tapering slightly above, anther-cells subglobose, 0.2 mm. long; bracts rather slenderly stalked, heads peltate, to 0.5 mm. across, these and perianths ciliate; peduncle (7–)15–22 × 3 mm., indumentum as twigs; *female head* with peltate bracts mostly shed and styles exserted to 1–2.5 mm. through conical papillae. *Syncarp* to c. 6 cm. across, globose, shallowly lobed, drying brown, the surface papillate or becoming nearly smooth, pubescent, with scattered persistent bracts; wall c. 2 mm. thick; proximal region of peri-

anths free, fruiting perianths numerous, thin-walled, "seeds" (indurated endocarps) subglobose, 14 mm. across; core c. 30 mm. across; peduncle 40(?)–75 × 5–7 mm., indumentum as twigs.

DISTRIBUTION: in forest to 1000 ft.; Philippine Islands.

Philippine Islands. LUZON. Zambales: Mt. Pinatubo, *Fox* PNH 4677 (A, ♀). Camarines: *Alvarez* FB 21235 (K, US, ♀). Sorsogon: *Curran* FB 10541 (BO, K), 10542 (NY, US, ♀), *Vidal* 3838 (K, ♀); Irosin, Mt. Bulusan, *Elmer* 16990 (A, BM, K, L, ♂, ♀). SAMAR. *Lasquety* FB 27032 (BO), *Ramos* 1604 (BM, BO, GH, L, P, SING, ♂), *Phasis* 25774 (P, ♀). LEYTE. *Rosenbluth* FB 12789 (K, NY, US, ♂, ♀), *Wenzel* 860 (BM, GH, ♂, ♀), 1576 (A, BM, GH, ♂); near Gacao, *Glassman* 794 (A, ♂, ♀); Palo, *Elmer* 7265, Jan. 1906 (A, BO, K, ♂). MINDANAO. Surigao: *Wenzel* 3297 (A, BO, GH, K, ♂), *Ramos & Pascasio* BS 34757 (NY, ♂).

The maximum size attained by the male inflorescence in this species is considerably larger than in any other species of subgenus *Pseudojaca*, but the dimensions of both the head and the peduncle are rather variable. However, the characteristic, broad, long-petiolate leaves enable male and sterile collections to be assigned to this species with certainty. The well-exserted styles at anthesis and the large syncarps, usually with long peduncles (but measuring only 7 mm. at anthesis in *Glassman* 794, cf. the male inflorescence), are equally distinctive. Older leaves and twigs are often almost completely glabrescent, and, since growth usually occurs in flushes, there may be a considerable difference in appearance between young and old shoots.

[To be concluded]

